2001

Predation by the exotic cladoceran Cercopagis pengoi on the zooplankton community of Lake Ontario.

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Predation by the exotic cladoceran *Cercopagis pengoi* on the zooplankton community of Lake Ontario

by
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A Thesis
Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
in Partial Fulfillment of the Requirements for the Degree of

Master of Science

at the University of Windsor
Windsor, Ontario, Canada

2001

945331

Abstract

The Ponto-Caspian cladoceran *Cercopagis pengoi* (fishhook waterflea) was first discovered in Lake Ontario in 1998. In 1999, it had spread to 5 Finger Lakes in upper New York State and to upper and lower Lake Michigan. By 2001, it was found in western Lake Erie. *Cercopagis* was transported to North America in ballast water of a transoceanic shipping freighter.

A survey of zooplankton community composition of Lake Ontario was made to assess the impact of *Cercopagis* predation. The relative abundance of zooplankton species of Lake Ontario has not changed from the early 1980's. However, *Cercopagis* has affected the species community composition through decreased abundances of total rotifers and major crustacean species such as *Bosmina longirostris*, *Daphnia retrocurva* and *Diacyclops thomasi*.

Laboratory experiments were conducted to determine possible prey species of *Cercopagis*. *Cercopagis* is able to prey upon the rotifer *Asplanchna priodonta* and the cladocerans *Bosmina longirostris*, *Daphnia retrocurva*, *Ceriodaphnia lacustris*, *Scapheloberis kingi*, *Moina micrura* and *Leptodora kindtii*.

In situ field experiments were conducted to assess natural zooplankton community impacts. Four different experiments failed to detect significant differences between control and predator treatments, thus predatory effects of *Cercopagis* were not apparent. Lack of predatory events may be attributed to experimental design. Problems that may have affected results include improper light levels, animal stress, mutual interference by *Cercopagis* individuals, and mortality of experimental *Cercopagis*.

Acknowledgements

I would like to express my sincerest gratitude to Dr. Hugh MacIsaac for giving me the opportunity to undertake my project. He allowed me to take on this project after I had completed the first year of my Master's under another supervisor. His guidance and patience gave me the perservance and insight needed to complete my thesis.

I would like to thank my committee members Dr. Weis, Dr. Haffner, Dr. Reitsma and my chair Dr. Heath for constructive ideas and comments.

I could not have completed my project without the help of Dr. Igor Grigorovich, whose vast knowledge and skill aided in the development of all of my experimental methods. His insight and help over the duration of my time here has been greatly appreciated.

I would like to acknowledgement the assistance of Sonja Vernooij. Her experience, ideas and assistance in laboratory and field experiments helped make this thesis possible. Her patience with me during our stay in Hamilton and at the Canadian Centre for Inland Waters will not be forgotten. Special thanks go to Andy Bramburger, Rob Colautti and Colin van Overdijk for help in the field survey and to Derek Gray, who aided in my 2001 experiments.

Thanks to all my labmates, Sarah Bandoni, Julianna Borbely, Tom Therriault, Helene Limen, Nancy Macdonald and Erin Copeland for an enjoyable time and stimulating conversations.

I am grateful to Dr. Ora Johannsson and Kelly Bowen for laboratory use at CCIW.

This research has been financially supported by a New York Sea Grant to HJM.

I dedicate this work to

my mother Jeanine, she has always been there for me

and to Shelley, who brought me lunch.

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Introduction

Freshwater lakes of the world are constantly bombarded by invasive, nonindigenous species (NIS). NIS, or exotic species, are successfully reproducing organisms which are transported to regions where they were not found previously (Mills *et al.* 1993). NIS are being spread amongst aquatic ecosystems worldwide through human-mediated activities, notably ballast water transport (e.g. Locke *et al.* 1991, Carlton and Geller 1993, Ruiz *et al.* 1997). The movement of NIS represents the single most significant threat to indigenous species in lakes throughout the world (Hall and Mills 2000, Sala *et al.* 2000). The introduction of a NIS may impact human health and economy, as well as ecosystem structure, diversity and function (Hall and Mills 2000, Pimentel *et al.* 2000).

Prediction of the success of a NIS invasion is of utmost importance in the prevention of future invasions (Ricciardi and Rasmussen 1998). Unfortunately, the unpredictability of biological invasions makes predictions of successful NIS almost impossible (Williamson and Fitter 1996). There are three NIS invasion phases: introduction, establishment and explosive population growth such that the NIS becomes a pest species (Williamson and Brown 1986, Williamson 1993). These levels are considered as 'steps of invasion' according to the 'tens rule' (Williamson and Fitter 1996). First, there is approximately a 1 in 10 chance of a NIS being introduced to a novel environment; second, 1 in 10 introduced NIS become established and reproduce; and lastly, 1 in 10 established NIS become pests and negatively impacting the novel region (Holdgate 1986, Williamson and Brown 1986). Although the 'phases' are simplistic, invasion models may serve as 'stepping stones' towards determining and quantifying species invasion dynamics (Williamson and Fitter 1996).

The rate of NIS dispersal is increasing with anthropogenic activity, especially shipping (Carlton 1985, Mills *et al.* 1993). Movement of NIS through transoceanic shipping activities is currently increasing in response to expansion of global trade. For example, ballasted shipping freighters release upward of 800 million liters of ballast water each year into the North American Great Lakes (Locke *et al.* 1993). Ballast water may contain an array of aquatic species, including various life cycle stages of algae, invertebrates and fishes, any of which may successfully establish in waters where ballasted water is released (Carlton and Geller 1993). However, the potential for successful invasion of any NIS depends upon a favourable environment and a suitable inoculum (Williamson 1993, Ricciardi and Rasmussen 1998).

Introductions of numerous Ponto-Caspian NIS in the Great Lakes-St. Lawrence region have been exacerbated by the creation of geographic 'invasional corridors' (Fig.1) (Ricciardi and MacIsaac 2000, Cristecu *et al.* 2001, MacIsaac 2001). These invasion corridors link Eurasia, via transoceanic shipping activities, with the Great Lakes ecosystem. Ricciardi and MacIsaac (2000) proposed three invasional corridors from the Ponto-Caspian region to North America: directly through the Mediterranean Sea from Black or Azov Sea ports; through the Dnieper River and Pripet-Bug canal system into the Baltic Sea via the Vistula or Neman rivers; and through the Danube River and Rhine-Main-Danube canal, via the Rhine River, through shipping ports on the North Sea. The latter two corridors are indirect, in that they require invaded Baltic or North Sea habitats to serve as donors to the Great Lakes. These corridors are almost exclusively uni-directional vectors from Europe to North America, as most ballast water moves from Eurasia to the Great Lakes. However, some species native to North American waters

have invaded European inland lakes (Kinzelbach 1995, Olenin and Leppäkoski 1999). Examples of these species include *Rhithropanopeus harrisi*, an invader in the Dnieper-Bug estuary, and both *Mercierella enigmatica* and *Mnemiopsis leidyi* which are North American invaders of the Black Sea (Karpevich 1975, Pereladov 1983).

The Great Lakes-St. Lawrence River system is subjected to an inordinate amount of 'propagule pressure' due to shipping activities (Williamson and Fitter 1996). Propagule pressure is the rate at which 'propagules', such as seeds and reproducing individuals, are released into the ecosystem. These ecosystems have been colonized by at least 160 NIS, with over 30 attributed to ballast water movement (Mills *et al.* 1993, Leach 1995, Witt *et al.* 1997, Zaranko *et al.* 1997, Ricciardi 2001, *in press*). Included in these 160 NIS are 55 invertebrates and fishes, of which 55% are native to Eurasia (Mills *et al.* 1993). Species native to the Ponto-Caspian region (i.e. Caspian Lake, Black and Azov seas) have been the most recent NIS to establish in the Great Lakes (Ricciardi and MacIsaac 2000).

The Ponto-Caspian region is host to a diverse variety of aquatic species (Mordukhai-Boltovskoi 1979, Dumont 1998). Many of these species have wide tolerances to temperature and salt concentrations (i.e. they are often euryhaline). These wide tolerances facilitate many Ponto-Caspian species to spread readily and extensively. Ponto-Caspian invaders of the Great Lakes include *Dreissena polymorpha* (zebra mussel), *Dreissena bugensis* (quagga mussel), *Echinogammarus ischnus* (amphipod), and most recently, *Cercopagis pengoi* (fishhook waterflea) (Ricciardi and Rasmussen 1998, MacIsaac *et al.* 1999).

One of the most recent species to invade the Great Lakes is the predatory cladoceran *Cercopagis pengoi* (fishhook waterflea), a native of the Ponto-Caspian region (MacIsaac

et al. 1999). *Cercopagis* is a native to the Black, Azov and Aral Seas, as well as the Caspian Lake (Rivier 1998, MacIsaac *et al.* 1999). *Cercopagis* has dispersed via human and natural vectors from its native range to other locations in Eurasia (Fig. 2). Aided by extensive canal and reservoir construction, *Cercopagis* has dispersed throughout eastern Europe via the Dnieper, Don and Manych rivers (Tseeb 1964, Zhuravel 1965, Mordukhai-Boltovskoi and Galinskiy 1974, Mordukhai-Boltovskoi 1979) (Fig. 2). By 1992, *Cercopagis* was found in the eastern Baltic Sea (Ojaveer and Lumberg 1995) and, subsequently, has been noted throughout the open-water and coastal regions of the Baltic Sea proper (Krylov *et al.* 1999, Uitto *et al.* 1999, Duris *et al.* 2000, Gorokhova *et al.* 2000).

Cercopagis was carried in ballast water to the Great Lakes. It was first discovered in Lake Ontario during summer 1998 (MacIsaac *et al.* 1999), when large groups of individuals were found as 'boluses' on sport-fishing downrigger lines. By 1999, it had invaded sites in upper and lower Lake Michigan and 5 Finger Lakes in upper New York State. During summer 2001, it was observed in western Lake Erie (Dr. I. Grigorovich, *pers. comm.*) It is likely to be spread further within the near future owing to its ease of movement by human vectors (Grigorovich *et al.* 2000) (Fig. 3).

Cercopagis is a freshwater species, but it exhibits broad tolerance to a wide range of salt concentrations (i.e. it is euryhaline) (Avinski 1997). Owing to its euryhalinity, it is able to invade both fresh and brackish waters (e.g. the Baltic Sea (Ojaveer and Lumberg 1995). *Cercopagis* has been found in water ranging from 8°C to 30°C, with an optimum range of 20°C to 25°C, at which it reaches its highest density (Mordukhai-Boltovskoi and Rivier 1987, K. McPhedran, *unpublished data*). *Cercopagis* reproduction is bicyclic,

with both asexual and sexual phases. Parthenogenetic females dominated populations in the Black and Baltic Seas and in Lake Ontario in July 1997 and August 1998 (Grigorovich *et al.* 2000). Sexual females produce resting eggs that over-winter and produce first-generation *Cercopagis* the following spring.

Two subgeneric forms of the genus *Cercopagis*, *Cercopagis* (*Apagis*) *ossiani* and *Cercopagis* (*Cercopagis*) *pengoi* have been recognized in Lake Ontario. The forms differ in structure and length of the caudal process, with only *Cercopagis pengoi* having a distinctive loop (Sars 1897, Mordukhai-Boltovskoi 1968, Mordukhai-Boltovskoi and Rivier 1987). It has been speculated that *Cercopagis* (*Apagis*) *ossiani* is a vernal form of *Cercopagis* (*Cercopagis*) *pengoi* that arises from resting eggs (Simm and Ojaveer 1999, Makarewicz *et al.* 2001). Both the *C. pengoi* and *C. ossiani* forms were present in Lake Ontario until late June 1999, after which only *C. pengoi* was found for the remainder of the year (Makarewicz *et al.* 2001). Genetic analysis of the ND5 mitochondrial gene revealed that *C. pengoi* and *C. ossiani* were genetically identical, suggesting that the two forms are actually a single taxon (Cristescu *et al.* 2001, Makarewicz *et al.* 2001). According to taxonomic nomenclature rules, the ancestral name -*Cercopagis pengoi*- applies to all individuals.

European workers have described the feeding mode and estimated clearance rates (volume of water swept clear of prey per predator per hour) of *Cercopagis* (Mordukhai-Boltovskoi 1968, Rivier 1998, Telesh *et al.* 2001). Based upon its morphology, *Cercopagis* is assumed to prey on zooplankton by tearing the integument and ingesting its contents (Mordukhai-Boltovskoi 1968); it may also have the ability to consume whole, soft-bodied prey (K. McPhedran, *unpublished data*). Despite a paucity of data, it has

been assumed that *Cercopagis* consumes nauplii, copepodites and adult calanoid copepods (Rivier 1998). Speculation about *Cercopagis*' feeding behaviour has resulted from extrapolation of study results for the confamilial *Bythotrephes cederstroemi*, a morphologically-similar exotic predator (Telesh *et al.* 2001). *Bythotrephes* has been shown to have strong effects on the zooplankton community of Harp Lake, Ontario (Yan and Pawson 1998). *Bythotrephes* has also changed species composition and decreased cladoceran abundance in Lake Michigan (Lehman and Cãcares 1993).

The assessment of the impact of a predatory species, such as *Cercopagis*, is an arduous task. The impact of the *Cercopagis* invasion in Lake Ontario (or anywhere else) has yet to be quantitatively ascertained. Recently, Telesh *et al.* (2001) employed a bioenergetic approach to estimate that *Cercopagis* could have strong effects on zooplankton in the Baltic Sea. However, its role as a zooplankton predator in Lake Ontario is unknown and is the subject of this thesis.

Cercopagis as a prey species of planktivorous fishes of Lake Ontario has yet to be ascertained. During 1999, it was found in alewife stomachs in Lake Michigan (Charlebois *et al.* 2001). In its Eurasian range, *Cercopagis* is a major component in the diet of Baltic herring (*Clupea harengus membras*) and a minor component in the diet of three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*) and smelt (*Osmerus eperlanus*) (Ojaveer and Lumberg 1995). Likewise, *Bythotrephes* is preyed on by adult lake herring (*Coregonus artedi*) (Coulas *et al.* 1998), alewife (*Alosa pseudoharengus*), perch (*Perca flavescens*) and rainbow smelt (*Osmerus mordax*) in the Great Lakes (Mills *et al.* 1993). However, feeding is limited in juvenile fish due to *Bythotrephes'* long caudal appendage that impedes swallowing attempts in

gape-limited fish (Barnhisel 1991). Similar problems may exist for *Cercopagis*, since crustaceans with extended caudal appendages take up to 8 times longer to swallow over those without (Rivier 1998).

Overall, the position of *Cercopagis* in the Lake Ontario food web is unknown. It may be an energetic link or sink within the zooplankton community. As an energetic link, it would consume herbivorous zooplankton species and then itself be consumed by planktivorous fishes. As an energetic sink, it would consume small zooplankton and competitively depress abundance of small planktivorous fishes, while avoiding predation due to its long caudal process (Makarewicz *et al.* 2001).

The objective of this thesis was to assess *Cercopagis*' effects on the Lake Ontario zooplankton community. Questions addressed include: Which zooplankton species do *Cercopagis* prey on? How has *Cercopagis* affected zooplankton size structure? What clearance and consumption rates are *Cercopagis* capable of? Is *Cercopagis* an energetic link or sink in Lake Ontario? What effects may *Cercopagis* have if it is spread to other lakes?

The hypothesis tested was that *Cercopagis* predation has no significant effects on the zooplankton community composition of Lake Ontario. I tested the hypothesis by comparison of temporal samples of the Lake Ontario zooplankton with historical zooplankton community compositions. I use laboratory experiments of the predation effects (consumption and clearance rates) of *Cercopagis* on predominant zooplankton species. Finally, I conducted *in situ* experiments to assess *Cercopagis* predation on natural zooplankton community of Lake Ontario.

Methods

Field Survey

Site description and sample collection

During May through October 2000, five sites in the western basin of Lake Ontario were sampled to assess zooplankton community composition. These included sites offshore (>5km) from Oakville (43°21'34N, 79°42'94W), Burlington (43°18'43N, 79°47'14W), Hamilton (43°17'34N, 79°45'15W), Stoneycreek (43°16'28N, 79°42'85W) and Grimsby, Ontario (43°10'01N, 79°42'52W) (Fig. 4). The five seasonal sampling sites were chosen to be representative of the western end of Lake Ontario (Fig. 4). The physicochemical and biological values taken from each of the five sites were categorically grouped, based upon corresponding surface depths, producing a single overall mean with standard error (where applicable). The Burlington site, at 8m, is representative of the near-shore, littoral zone. The Hamilton site, at 30m, is representative of the near-shore, pelagic zone. The remaining sites were intermediate, ranging in depth from 10 to 20 metres.

At all sites three replicate plankton samples were taken using both 53μm and 253μm Nitex mesh (0.5m diameter, 4:1 length: diameter ratio) plankton nets. The use of different Nitex mesh sizes allows for fractionating of the zooplankton community into two size assemblages. Specifically, the 253μm mesh allows for quantitative capture of large rotifers (e.g. *Asplanchna priodonta*), adult cladocerans and copepodids and copepods. The larger mesh has a higher capture efficiency for large plankton, but is ineffective at capturing smaller taxa. However, later sample enumeration becomes

simpler for samples collected with this mesh size owing to fewer organisms, less phytoplankton and detritus in the samples. A 53μm mesh allows for quantitative capture of small plankton including most rotifers and small cladocerans. However, the finer mesh size has a lower filtering efficiency and can become clogged and consequently allow escape of large, fast-swimming zooplankton. Sample enumeration is more difficult than with 253μm mesh nets owing to the presence in some samples of large amounts of detritus and phytoplankton.

Sampling was done between 8 AM and 6 PM on all dates. Variation in sampling time was dependent upon lake conditions and travel time. Zooplankton samples were collected using vertical hauls taken from 2m below the thermocline (if present, 2m from lake bottom when no thermocline was present). Sampling depth is based on the reported predominately epilimnion-water distribution of *Cercopagis* (Krylov *et al.* 1999, Ojaveer *et al.* 2001). All samples were placed into 250ml or 500ml mason jars and preserved using 95% ethanol (approximately 70% ethanol final concentration). Repeated samples of each mesh size were physically combined for each site prior to enumeration.

Sample enumeration

Plankton samples were individually concentrated or diluted to usually obtain 100 –300 organisms per subsample, with rare cladoceran species (e.g. *Leptodora kindtii*) being counted *in toto*. Samples were mixed thoroughly prior to subsamples (between 0.5ml and 2ml) being drawn off using a Nichiryo Model 5000 pipette. In most cases, at least two pipetted volumes were placed within each subsample counting chamber. Counting chambers were 2, 4, or 6 ml in size, and were used according to sample organism

densities. For subsample counts, a Medilux-12 compound microscope (100X) was used for enumeration, while a Leica Wild M8 dissecting microscope (20-30X) was used for *in toto* enumeration. Two such subsamples were taken (with replacement) for each sample site and mesh size. The coefficient of variation was calculated for the two replicate subsamples, and if the value exceeded 10% a third subsample was then collected and enumerated. *Cercopagis pengoi* and *Cercopagis ossiani* were counted *in toto*, using fine forceps to separate large boluses that occurred in mid-summer samples.

Crustacean zooplankton were identified using Balcer *et al.* (1984). Rotifer species were identified using Stemberger (1979).

The density of organisms was calculated as the number of individuals per cubic metre (I) according to the following equation:

$$I = (C * SB / SV) * \frac{1}{3\pi r^2} * \frac{1}{D}$$ where: Eqn. 1

C= individuals in subsample count
SV= subsample volume
SB= total sample volume
r= radius of plankton net (0.25m)
D= depth of vertical haul (m)

*Note: the 3 is used to correct for the combination of three repeated samples at each site prior to enumeration.

Physicochemical parameters

Parameters were measured at each site in 1m intervals until 2m below the thermocline (when present), or to 2m above the lake bottom when the lake was not stratified. A Hydrolab Datasonde® 4A water quality multiprobe was used to measure temperature (°C), dissolved oxygen (mg/L), conductivity (μS/cm), total dissolved solids (g/L), pH,

salinity (ppt) and turbidity (NTU). The Hydrolab® was used to determine site depth. Secchi disc transparency was measured to assess light transmission.

Laboratory Experiments

Parameters

All experimental lake water used in laboratory containers was collected using 22.5L carboys filled directly from the water surface (unless otherwise stated). All lake water was filtered using a Whatman glass microfibre 934AH filter (1.5μm) and post-filtered to remove all zooplankton using a 43μm Nitex mesh. All zooplankton experiments were conducted in a controlled-environment chamber at 18°C and 1.79$\mu E*m^{-2}*s^{-1}$ light intensity (24 hour light). Zooplankton for experimental use were identified, separated and observed with Leica Wild M8 and ZeissJena Technival 2 dissecting microscopes (10-20X). All *Cercopagis* and prey species used in laboratory experiments were processed according to the acclimation and prey collection procedures outlined below. All *Cercopagis* individuals used were 3rd instar, parthenogenetic female adults, unless otherwise stated. All samples were preserved using 95% ethanol.

Acclimation Procedure

Third instar parthenogenetic female *Cercopagis* were collected daily from eastern Hamilton Harbour using bottom to surface hauls (<2m) of a 0.5-m-diameter, 500μm Nitex mesh plankton net. Zooplankton samples were rinsed from the net, using lake water, into 1.5L containers. Containers were subsequently completely filled with water in an attempt to minimize stress during transport to the laboratory. Samples were poured

into 9cm petri plates for examination with the dissecting microscopes. Free (i.e. spine unattached to conspecifics or detritus) *Cercopagis* individuals were isolated and removed from samples using either a wide mouth pipet or fine forceps (cradled), depending on body size. Individuals were placed singly into 150ml jars filled with filtered lake water. *Cercopagis* individuals were allowed to acclimate to laboratory conditions within the controlled environment chamber for a 24 hour period, prior to the addition of prey. Preliminary experiments without acclimation led to >90% mortality of *Cercopagis* with no predation effects. Yurista and Schulz (1995) also used a 24 hour acclimation of *Bythotrephes* prior to experimental use. Thereafter, at the onset of each laboratory experiment, only healthy individuals were utilized in laboratory treatments.

Prey collection procedure

Prey species were collected from eastern Hamilton Harbour using bottom to surface hauls (n=5, <2m) of a 0.5-m-diameter, 53μm Nitex-mesh plankton net. Individual prey species were separated into monocultures by use of a dissecting microscope. Species monocultures were placed in 2L containers filled with aerated, filtered lake water within the controlled environment chamber. Prey were fed dried *Chlorella* daily (<1mg/L). Every second day, prey monoculture water volumes were reverse filtered to 25% of the total initial volume using a 40μm Nitex mesh filter, and brought back up to volume with the addition of freshly-collected, filtered lake water. This procedure allowed for the maintenance of most prey species throughout the laboratory experiments.

Zooplankton species present in harbour samples at low abundance were collected from two local ponds (Ojibway and Malden parks) in Windsor, Ontario. Prey species were

collected using mesh screens, rinsed into jars, and then maintained as the above species monocultures.

Laboratory experimental outlines

Eight prey species representing one rotifer (*Asplanchna priodonta*) and seven cladoceran taxa (*Ceriodaphnia lacustris, Scapheloberis kingi, Bosmina longirostris, Moina micrura, Leptodora kindtii, Daphnia retrocurva, Polyphemus pediculus*) were used to test zooplankton vulnerability to *Cercopagis* predation. Experiments were conducted in both small and large vessels (see below).

Small vessel

Small container treatments included prey species presented individually with a single *Cercopagis*. Prey species treatments included *Daphnia retrocurva, Ceriodaphnia lacustris, Asplanchna priodonta, Scapheloberis kingi* and *Moina micrura*. Prey individuals (10 each) were assessed for vigour (under a dissecting microscope) and randomly added to 150ml containers filled with filtered lake water. There were three replicates for each species treatment and each received a single *Cercopagis* individual. Replicate controls without *Cercopagis* were also run for each treatment. Containers were placed in an open-top box allowing only diffuse overhead light within the controlled environment chamber. After 18 hours, treatments were observed using dissecting microscopes to assess predator and prey mortality, and animal condition. Prey individuals found in surface film were considered as live after the experimental period. Samples were preserved using 95% ethanol.

Large vessel

Treatments were identical to those conducted in small vessels, except that volume size was 1.5L, 40 prey individuals were added to each container (5 replicates) and experiments were 12 hours in duration. Prey species treatments included *Ceriodaphnia lacustris*, *Daphnia retrocurva* and *Bosmina longirostris.*

Cannibalism

Single 1st, 2nd, and 3rd instar *Cercopagis* individuals were assessed for vigour and transferred to 150mL containers filled with filtered lake water according to the following treatments: 1st instar with 2nd instar, 1st instar with 3rd instar, 2nd instar with 3rd instar and 3rd instar with 3rd instar, respectively. All trials were replicated 5 times. After 24 hours, individuals were observed using a dissecting microscope to assess mortality and condition. Samples were preserved using 95% ethanol.

Predator vs. Predator interactions

Predatory zooplankton species presented as potential *Cercopagis* prey included *Leptodora kindtii* and *Polyphemus pediculus*. Predator species were collected and maintained according to the *Cercopagis* collection and acclimation procedure (see above). Prey individuals were added singly to 150ml containers filled with filtered lake water, each containing a single *Cercopagis* individual. There were 5 replicates for each species treatment. Containers were observed using dissecting microscopes to assess predation events, mortality and condition after 12 and 24 hours. Samples were preserved using 95% ethanol.

Imaging Analysis

The size structure of prey was determined through random subsampling of at least 10 individuals for each species used in experimental treatments. Body length measurements were made using Optimas 6.2 imaging software, linked to a Hitachi D.S.P. color video camera operating through a Medilux-12 compound microscope. Body lengths were measured from tip-of-head to base-of-tailspine for *Daphnia* and tip-of-head (or body) to the posterior carapace (or body) for *Ceriodaphnia, Asplanchna, Moina, Scapheloberis* and *Bosmina.*

Electivity Indices

The estimation of *Cercopagis* clearance rates of individually presented zooplankton prey species in laboratory experiments can be combined and processed for use in the determination of the relative preference of individual prey species when multiple species are presented simultaneously (Chesson 1978). Laboratory clearance rates were based on the following model:

$$c_i = \frac{M}{Ct} * \ln \frac{n_{io}}{n_{it}} \qquad \text{(Coughlan 1969)} \qquad \text{Eqn.2}$$

where c_i is the volume of water a predator clears of prey type i per unit time, M is the volume of the test container, C is the number of predators, n_{io} is the number of initial prey individuals presented and n_{it} is the number of prey individuals at time t.

After calculation of individual clearance rates for different prey species, relative prey preferences (when many species are presented simultaneously) were estimated by:

$$\alpha_i = \frac{\hat{c}_i}{\sum_{j=1}^{n} \hat{c}_j} \qquad \text{(Manly } et\ al. \text{ 1972)} \qquad \text{Eqn. 3}$$

where α_i is the moment estimate of relative preference of the predator for each of i prey species presented. This preference index can be used to estimate clearance rates in experiments involving variation in both prey species densities and experimental duration. All clearance rate and preference calculations for laboratory experiments were determined after correction of surviving prey abundance in treatments against corresponding control values as follows:

$$p_i = (c_o - c_t) - (e_o - e_t) \qquad \text{Eqn. 4}$$

where p_i is the corrected prey number, c_o is the initial control prey, c_t is the final control prey, e_o is the initial experimental prey number and e_t is the final experimental abundance. Values of α_i range from 0 (negatively selected) to 1 (positively selected), with one divided by total number of prey species classes representing a neutral selection (e.g. 0.2 for 5 classes)(Chesson 1978).

Bioenergetic estimation

Bioenergetic models may be used in the estimation of prey consumption rates. Models have been valuable in the study of feeding by predatory invertebrate crustaceans including *Mysis relicta* (Rudstam 1989) and *Bythotrephes* (Yurista and Schulz 1995). Bioenergetic models may be developed based upon measured physiological energetic requirements such as consumption, ingestion, assimilation, respiration, exoskeletal moulting and growth and reproduction. These energetic requirements can be used to calculate the prey consumption rate needed to balance overall energetic needs. A

bioenergetic model was developed for *Bythotrephes* as follows (Yurista and Schulz 1995):

$$Consumption = \frac{(growth + respiration + moult)}{(ingestion\_efficiency * assimilation\_efficiency)} \qquad \text{Eqn. 5}$$

Each of the parameters of the consumption model is individually weighted based upon measured energy consumption characteristics. Total consumption model allows for the estimation of overall prey consumption rates needed to balance energetic needs.

The feeding behaviour of *Cercopagis* and *Bythotrephes* are quite similar. Both species grab prey with enlarged thoracopods and suck out body contents (Rivier 1998). As well, both species occupy approximately similar niches in zooplankton communities (Mordukhai-Boltovskoi 1968, Rivier 1998). Morphological features similar to the two genera include: 1) a single, compound eye, used for prey detection; 2) antennae II are biramous and used for swimming; 3) mandibles are adapted for biting prey; 4) the trunk has four pairs of thoracopods, used for grasping prey; 5) well-developed abdomen with an elongate caudal process extending greater than one body length; 6) caudal process with articular spines reflecting instar stage (Mordukhai-Boltovskoi and Rivier 1987). Owing to the paucity of physiological data for *Cercopagis*, the *Bythotrephes* model was used as a basis for estimation of *Cercopagis* consumption rates, with appropriate model adjustments based upon the proportional body mass of the two species. Average *Bythotrephes* mass was taken from the model developed by Yurista and Schulz (1995), and divided by the average 3rd instar *Cercopagis* mass for Lake Ontario samples (Grigorovich *et al.* 2000). The resultant proportional mass difference was used to convert

consumption rates of *Bythotrephes* (Yurista and Schulz, Table 2, 1995) to those of *Cercopagis* (Table 12). Median lengths and estimated masses of prey species were obtained from Bottrell *et al.* (1976) and Culver *et al.* (1985).

Field experiments

Manipulated assemblage

For the manipulated *in situ* experiments, *Cercopagis* individuals were collected and handled as in the laboratory experiments described above. Single *Cercopagis* individuals were placed in 150ml 'holding' containers filled completely with filtered lake water (as above) that minimizes water current effects caused by air pockets. *Cercopagis* was acclimated, without prey, to field conditions in eastern Hamilton Harbour water at approximately 2m below the water surface for 24 hours prior to use in experiments. One *Cercopagis* and 15 randomly picked individuals of each prey species (*Ceriodaphnia*, *Daphnia*, *Bosmina* and *Chydorus*) were added to 2L Gladware™ containers that had been completely filled with filtered lake water (5 replicates and 3 controls lacking *Cercopagis*). Containers were placed approximately 2m below the surface, tethered to the dock at the Canadian Centre for Inland Waters (CCIW), in eastern Hamilton Harbour (Fig. 5). After 24 hours, containers were retrieved and their contents concentrated by reverse filtration, using a 40μm Nitex mesh filter to prevent loss of animals. Contents were examined using a dissecting microscope to assess mortality of predators and prey, and animal condition. Treatments were preserved using 95% ethanol.

Natural assemblage

Year 2000- Field experiments 1 and 2

Cercopagis was collected from eastern Hamilton Harbour, as above, except that individuals were assessed for health and placed individually into 20ml scintillation vials filled with filtered lake water. Individuals used in the natural assemblage experiments were added to experimental treatments without being acclimated to field conditions. Lake water used in all treatments was collected from the near-shore zone of western Lake Ontario using a 20L Schindler-Patalas trap opened at 2m below the water surface. Lake water was placed in 75L holding chambers before being pre-filtered into the treatment carboys (22.75L) through a 750μm Nitex mesh. To ensure that zooplankton densities were as similar as possible at the experimental outset, carboys were filled by sequential additions of 4L aliquots. The 750μm mesh pre-filter was chosen since it retained all *Cercopagis*, while allowing passage of most prey species. Treatments included five replicates each of 0-hr control, 24-hr control and 24-hr with 10 *Cercopagis* (Fig. 6). Experiments lasted 24 hours, since *Cercopagis* individuals have been shown to remain in the epilimnion throughout day and night periods, as does the closely related *Bythotrephes* (Vanderploeg *et al.* 1993, Ojaveer *et al.* 2001). Zero hour controls were immediately filtered using 40μm Nitex and preserved in 95% ethanol, to determine zooplankton abundance of the prey assemblage at the outset of the experiment. All 24-hour treatments were tethered 2m below the water surface in eastern Hamilton Harbour off the dock of CCIW (Fig. 6). After 24 hours, all remaining carboys were filtered using 40μm Nitex and preserved using 95% ethanol. The natural assemblage experiment was duplicated on August 10th and 16th, 2000 and on July 5th and August 2nd, 2001. Field experiment #1

utilized 3rd instar *Cercopagis*, while #2 used both 1st and 2nd instar *Cercopagis* in different treatments.

Year 2001- Field experiments 3 and 4

Field experiments #3 and #4 were conducted as above, using only 3rd instar *Cercopagis*. However, experiments were conducted in 4L clear plastic containers, with sequential aliquots of 0.5L lake water added to each container. Field experiment #3 was conducted for 24hr, using a 750μm Nitex-mesh pre-filter. Treatments included five replicates each of 0-hr control, 24-hr control and 24-hr with 4 *Cercopagis*. Field experiment #4 was conducted for 48hr, using 1mm Nitex-mesh pre-filter. Treatments included five replicates each of 0-hr control, 48-hr control, 48-hr with 4 *Cercopagis* and 48-hr with 8 *Cercopagis*.

Statistical Analysis

Experimental abundance data were ln (x + 1) transformed prior to statistical analysis using Systat (Version 8.0) for Windows. Values were transformed to stabilize sample variance. A General Linear Model was used to analyze differences between treatments, with *Cercopagis* treatment as the independent, categorical variable for each model (Systat 8.0). Univariate tests (ANOVA) and multivariate tests (MANOVA) were performed for each field experiment. For each treatment total rotifers, total cladocerans, total copepods, copepod nauplii, *Dreissena* veligers, and total zooplankton were compared separately, when applicable. If significant differences were detected, Bonferroni multiple comparison tests (at α= 0.05) were utilized to explore the nature of the differences. Significant differences between 0 and 24-hr (or 48-hr) controls would reveal possible

container effects. Significant differences between 24-hr (or 48-hr) control and 24-hr (or 48-hr) *Cercopagis* treatments would reveal predation effects.

Results

Field Survey

Dissolved oxygen (mg/L) levels ranged from a minimum of 10mg/L during August and October to a maximum of 13mg/L starting in late May through July (Fig. 7). Dissolved oxygen content showed no apparent stratification and minimal variation throughout the water column.

The near-surface water temperature (°C) increased from a minimum of 8°C in early May to a (single site) maximum of 21°C in mid-August (Fig. 7). The water column was unstratified during May and October. During June, July and August the lake exhibited a thermocline occurring at approximately 7-10m (Fig. 7).

Overall pH values ranged from a low of 9.1 in May to a high of 9.7 during June and July (Table 1). Conductivity (μs/cm) values showed almost no variation over the sampling period (Fig. 8). Secchi depth (m) values averaged 4.5m during May, decreased to 3.6m during the month of June and then increased and stabilized at approximately 5.5m for the remaining sampling period.

All abundant rotifer species exhibited peak abundance during July, except the rotifer *Trichocerca multicrinis*, which was most abundant on June 27th (Fig. 9, Table 2). On this date, *Trichocerca* accounted for 50.0% of all rotifers, with an abundance of 22,690 (±6119) Ind./m^3. Four other rotifer species accounted for at least 10% of the total rotifer community during July (Table 2). On July 3rd, *Polyarthra remata, Kellicottia longispina* and *Keratella cochlearis* accounted for 14.9%, 25.3% and 33.9% of total rotifers, with abundances of 8,598 (±2421) Ind./m^3, 14,626 (±3370) Ind./m^3 and 19,528 (±4989)

Ind./m^3, respectively. On July 27th, *Keratella crassa* accounted for 51.2% of total rotifer abundance, at 21,905 (±6591) Ind./m^3 (Fig. 9).

Total rotifer abundance peaked on July 3rd, at 57,840 (±13,837) Ind./m^3. During this peak abundance, rotifers accounted for 99% of the total zooplankton abundance. All rotifer species exhibited a single abundance peak on a sampling date that was markedly different from all other dates (Fig. 9). Overall total rotifer abundance was less than 5,000 Ind./m^3 until June 19th, increasing to its peak abundance on July 3rd and then returned and stabilized at less than 5,000 Ind./m^3 by August 10th.

Five crustacean species accounted for at least 10% of total crustacean abundance during the sampling period (Table 2). On August 10th, *Cercopagis pengoi* and *Eubosmina coregoni* accounted for 29.6% (96±37 Ind./m^3) and 10.8% (35±19 Ind./m^3) of total crustaceans, respectively. On August 24th, *Bosmina longirostris* accounted for 49.6% (476±143 Ind./m^3) of total crustaceans. On October 4th, *Daphnia retrocurva* and *Diacyclops thomasi* accounted for 50.6% (876±217 Ind./m^3) and 42.2% (731±202 Ind./m^3) of total crustaceans, respectively (Fig. 10).

Total crustacean abundance peaked on October 4th, at 1730 (±325) Ind./m^3 (Fig. 10). At peak abundance, crustaceans accounted for 22% of the total zooplankton community. *Cercopagis* abundance peaked during August, with abundance at least 10 times higher than that of any other month. *Bosmina longirostris, Leptodora kindtii, Eubosmina coregoni* and copepod nauplii abundances all reached peak abundances and then decreased simultaneously in parallel to *Cercopagis* abundance changes (Fig. 10). *Diacyclops, Daphnia* and total crustacean abundances did not increase to their maximum

abundance values until after *Cercopagis* abundance waned. *Bosmina* had two apparent abundance peaks, occurring on July 3rd and August 24th (Fig. 10).

Cercopagis (*Apagis*) *ossiani* was a relatively rare species, even when it was most abundant in the lake. For example, its peak abundance on May 5th was 0.6 (±0.2) Ind./m^3. *C. ossiani* was found until June 27, after which it was no longer detectable (Fig. 10). *Cercopagis* (*pengoi*) *pengoi* was first present on June 27, reached its maximum abundance during August exceeding 90 Ind./m^3 and was undetectable by October 4th (Fig. 10).

Laboratory Experiments

Small vessel

The prey density available for predation by *Cercopagis* in small container experiments averaged approximately 66,000 Ind./m^3. This value is equivalent to the peak total zooplankton abundance in western Lake Ontario (Figs. 8, 9).

In small container experiments, *Cercopagis* mortality was very high, with 10 of 15 individuals dying during the experimental period (Table 3). However, predation events still occurred in many of the treatments. The highest clearance rate calculated of any species was *Asplanchna priodonta*, at 0.091 L/*Cercopagis*/day (Table 5). The lowest clearance rate calculated was for *Moina micrura*, where reproduction of prey resulted in a clearance rate of 0 L/*Cercopagis*/day when corrected against control values. *Daphnia* treatments had evidence of predation events, with prey individuals missing entire body parts (e.g. head or post-abdomen). Missing prey individuals were considered consumed

totally, since personal observations concluded that *Cercopagis* might consume whole soft-bodied prey.

Large vessel

The density of prey organisms available for predation in the large containers equated to approximately 26,000 Ind./m^3, or approximately the average total zooplankton abundance in western Lake Ontario (See Figs. 8, 9).

In large container treatments, *Cercopagis* mortality was low, with 3 of 15 individuals dying during the experiments (Table 4). *Cercopagis* had similar clearance rates for *Bosmina longirostris* and *Daphnia retrocurva* treatments, at 0.113 and 0.107 L/*Cercopagis*/day, respectively (Table 5). Reproduction by *Ceriodaphnia lacustris* resulted in a corrected clearance rate of 0 L/*Cercopagis*/day, although evidence of predation was noted within the treatment (Table 4).

Electivity indices

Relative *Cercopagis* prey preference values were calculated for each species based upon clearance rate data (Table 5). Values close to zero, indicating negative prey preference, occurred for *Ceriodaphnia lacustris, Moina micrura* and *Daphnia retrocurva*, with values of 0.05, 0 and 0.05, respectively. Neutrally selected species included *Scapheloberis kingi,* with relative prey preference of 0.26. Only *Asplanchna priodonta*, with a preference value of 0.65, was positively selected.

Relative prey preference, as a function of prey species body size, is shown in Figure 10. There is a decreasing trend of preference for small and large prey species size, as shown by the regression line (Fig. 11)($y= -0.00005X^2+0.0187X-5.3376$, $R^2= 0.9014$).

Cannibalism

Higher (2nd or 3rd) instar *Cercopagis* had mortality in 4 of 15 replicates (Table 6). Lower (1st or 2nd) instar *Cercopagis* had mortality in 7 of 15 replicates. Overall, in all experimental replicates, 5 of 10 individuals in each of the 1st and 2nd instar treatments moulted during the experimental duration. Direct evidence of moulting, presence of an exuvium, was found in only four of these cases. Overall, two of the fifteen replicates had evidence for cannibalistic events (Table 6). A 2nd instar *Cercopagis* individual, which had molted into a 3rd instar, had consumed a 1st instar *Cercopagis* individual. The 3rd instar individual was found with a 1st instar individual spine and loose head. In the other cannibalism event, a 3rd instar *Cercopagis* individual was visualized with a 3rd instar *Cercopagis* caudal process.

Predator vs. Predator

Third instar *Cercopagis* mixed with *Polyphemus pediculus* resulted in no mortality of either organism. Predation events occurred when *Leptodora kindtii* and *Cercopagis* were put together. After 18 hours of incubation, *Cercopagis* had preyed upon 3 of 5 *Leptodora*. Of these, two *Leptodora* were consumed (or shredded) almost completely; as well, half a *Leptodora* individual remained in a third case. After 24 hours, the remaining two *Leptodora* and *Cercopagis* replicates showed no signs of predation by either species. Predation on *Leptodora* is surprising, considering it is a much larger species than *Cercopagis*.

Bioenergetics estimation

Estimated consumption rates on zooplankton species found in the current study were taken, when available, from Yurista and Schulz (Table 2, 1995). After correction was made for body mass differences between *Bythotrephes* and *Cercopagis* estimates of daily consumption needs of *Cercopagis* on various zooplankton species were determined (Table 13). Consumption rates for cladoceran species ranged from <1 Ind./*Cercopagis*/24hr for large *Leptodora kindtii*, to 11 Ind./*Cercopagis*/24hr for small *Ceriodaphnia lacustris* (Table 13). Rotifer estimates ranged from 18 Ind./*Cercopagis*/24hr for large, soft- bodied *Asplanchna priodonta*, to 198 Ind./*Cercopagis*/24hr for small-bodied *Polyarthra vulgaris* (Table 13).

Field Experiments

Manipulated assemblage

No significant differences between control and *Cercopagis* treatments were found (MANOVA, F=2.06, df=3,5, p>0.05, Table 7) with respect to prey abundances. However, for *Chydorus sphaericus* there were 13.2 (±1.7) individuals found alive after 24 hours in control treatments, while only 8.5 (±1.9) individuals were found in *Cercopagis* treatments.

Natural assemblage

Field experiment #1: 3rd instar

The most abundant rotifer species present were *Keratella cochlearis*, *Keratella crassa*, *Ploesoma truncatum*, *Polyarthra remata*, and *Polyarthra dolicoptera*, each of which

accounted for >10% of total rotifers in at least one replicate (Table 9). The most abundant crustacean species were *Bosmina longirostris* and cyclopoid copepod species, each accounting for >10% of total crustaceans in at least one of the replicates (Table 9). Total zooplankton abundance ranged from 275.6 Ind./L for the 24hr control treatment to 431.4 Ind./L for the 0hr control treatment. Total rotifers (ANOVA, $F= 6.98$, $df=2,6$, $p<0.05$) and *Dreissena* veligers (ANOVA, $F=14.4$, $df=2,6$, $p<0.05$) were statistically different (Table 12) between the 0-hr and 24-hr control treatments, with 24-hr treatments having higher abundances (Bonferroni's test).

Field experiment #2: 1st and 2nd instar

The most abundant rotifer species present were *Polyarthra remata, Keratella crassa, Ploesoma truncatum* and *Ascomorpha sultans*, each accounting for >10% of total rotifers in at least one replicate (Table 8). The most abundant cladoceran species were *Bosmina longirostris* and *Polyphemus pediculus*, each accounting for >10% of total cladocerans in at least one of the replicates (Table 8). Total zooplankton abundances ranged from 65.2 Ind./L for the 24hr 1st instar treatments to 74.6 Ind./L for the 0hr control treatments. No statistical differences were found with respect to cladoceran abundances between any treatments (Table 12).

Field experiment #3: 3rd instar

The most abundant rotifer species present were *Polyarthra remata, Polyarthra major* and *Ploesoma truncatum*, each accounting for >10% of total rotifers in at least one replicate (Table 10). Total zooplankton abundance ranged from 512.2 Ind./L for the

0-hr control treatment to 642.8 Ind./L for the 3rd *Cercopagis* treatment. No statistical differences were found between any treatments (Table 12).

Field experiment #4: 3rd instar

The most abundant rotifer species present were *Polyarthra remata*, *Polyarthra major* and *Ploesoma truncatum*, each accounting for >10% of total rotifers in at least one replicate (Table 10). Total zooplankton abundance ranged from 389.3 Ind./L for the 0-hr control treatment to 796.8 Ind./L for the 48-hr control treatment. Total rotifers (ANOVA, $F=8.44$, $df= 3,8$, $p<0.05$), total cladocerans (ANOVA, $F=8.08$, $df= 3,8$, $p<0.05$), total copepods (ANOVA, $F=14.6$, $df= 3,8$, $p<0.05$) and total zooplankton (ANOVA, $F=11.8$, $df= 3,8$, $p<0.05$) were statistically different (Table 12). All groups differed between 0-hr control and all 48-hr treatments, with 48-hr treatments being greater in all cases (Bonferroni's test). Thus, evidence of predation was lacking.

Discussion

The establishment of a NIS into a new environment provides ecologists with opportunities to examine effects of novel species on ecosystem structure and function. Effects of the invasion of the invertebrate cladoceran *Cercopagis pengoi* on the Lake Ontario zooplankton community have not been assessed previously. Determination of the impact of *Cercopagis pengoi* on native zooplankton composition of Lake Ontario was the goal of this study. *Cercopagis* has been speculated to consume nauplii, copepodites and adult calanoid copepods (Rivier 1998). However, these inferences were made in the absence of experimental feeding rate data. Based upon laboratory predation experiments and seasonal zooplankton abundance patterns in the lake, this study determined that *Cercopagis* may prey upon numerous Lake Ontario zooplankton species. Vulnerable species include the cladocerans *Bosmina longirostris*, *Ceriodaphnia lacustris*, *Scapheloberis kingi*, *Moina micrura*, *Daphnia retrocurva*, *Leptodora kindtii*, the rotifer *Asplanchna priodonta*, and the copepod *Diacyclops thomasi.*

The field survey of five sampling sites in the western basin of Lake Ontario was performed to monitor temporal and spatial abundances of native zooplankton and *Cercopagis*. By monitoring abundances, inverse patterns of zooplankton and *Cercopagis* abundances may be attributed to predation by the latter species. As well as tracking the abundances, comparison of assemblages to historical zooplankton patterns of spatial and temporal abundance may ascertain if *Cercopagis* has affected zooplankton community composition. *In situ* field experiments were performed in an attempt to determine the overall effect that *Cercopagis* predation may have on the Lake Ontario zooplankton

community. Amalgamation of these studies should allow for the prediction of the overall impact of *Cercopagis pengoi* on Lake Ontario's zooplankton.

Cercopagis in Lake Ontario

The field survey of zooplankton composition in Lake Ontario is useful to establish what impact, if any, *Cercopagis* is having on zooplankton community dynamics (Fig. 4). Small herbivores or microzooplankton have historically dominated Lake Ontario, suggesting intense planktivory by, notably, the alewife (*Alosa pseudoharengus*) (Lampman and Makarewicz 1999). Introduction of predatory invertebrates, such as *Cercopagis*, may serve as an energetic link within the zooplankton (Lampman and Makarewicz 1999). However, this holds true only if *Cercopagis* preys on herbivorous zooplankton and, in turn, is consumed by planktivorous fishes such as alewife, the dominant planktivore (Makarewicz *et al.* 2001). *Cercopagis* has been found in alewife stomachs both in Lake Ontario and Lake Michigan (Dr. E. Mills, *pers. comm.*, Charlebois *et al.* 2001). Consumption of *Cercopagis* by alewife will increase the energy transfer efficiency of the Lake Ontario ecosystem, in the absence of other large zooplankton (Mazumder *et al.* 1992).

The *Cercopagis ossiani* 'form' is unlikely to have marked effects on zooplankton community composition. Its maximum abundance of 0.6 Ind./m^3 was <1% of the *C. pengoi* form and it was only detectable in the plankton for approximately two months during May and June (Fig.9). The *C. ossiani* abundance decline could be attributed to increasing water temperature, longer daylight hours, predation by alewife, or to natural decline as the maximum lifespan was achieved. Moreover, *C. ossiani* individuals likely

produced *C. pengoi* offspring, thus there was no recruitment of a second generation of *C. ossiani*. Consequently, it is highly likely that *C. ossiani* represents a 'spring-form' morph hatched from overwintered resting eggs (Simm and Ojaveer 1999). Genetic analysis of *C. ossiani* and *C. pengoi* revealed that the species were genetically identical at the mitochondrial ND5 gene, suggesting that the two forms are a single, ontogenetic species (Makarewicz *et al.* 2001).

Cercopagis pengoi reached peak abundance during August, being at least 10 times higher during that month than at any other time (Fig. 10). During August, the surface water temperature exceeded 20°C, which is within the optimal range of 20-25°C for the species (Table 1) (Mordukhai-Boltovskoi and Rivier 1987). *Cercopagis* abundance peaked in August during 1998, 1999 and 2000 (MacIsaac *et al.* 1999, Makarewicz *et al.* 2001). The average maximum abundance reported for 1998 at the current study's sampling sites was 170 Ind./m^3, with a maximum of 322 Ind./m^3 (MacIsaac *et al.* 1999). The 2000 average maximum abundance was only 96 Ind./m^3, with a maximum of 268 Ind./m^3 (Fig. 10). The decline in maximum abundance may be attributed to lower surface temperature during 2000, as the mean value never exceeded 20°C (Fig. 7), whereas it exceeded 23°C during 1998 (Grigorovich *et al.* 2000). As well, abundance may have been lower due to higher alewife abundance and thus higher predation pressure on *Cercopagis* during 2000. Alewife abundance (+1 age) was at its lowest recorded level in 20 years during 1998 (Makarewicz *et al.* 2001). The lack of high abundance of the dominant predator may have allowed establishment and high population densities of *Cercopagis* in Lake Ontario. However, alewife abundance was higher in 2000, thus predation pressure may have been higher (Dr. J. Makarewicz, *pers. comm.*). Thus, lower

Cercopagis abundances during 2000 may have been due to temperature or predation by fish.

Comprehensive lake-wide sampling has occurred since the 1960's (Patalas 1969, Johannsson *et al.* 1991, Johannsson *et al.* 1998, Lampman and Makarewicz 1999). The most abundant rotifer species during the sampling period included *Keratella cochlearis*, *K. quadrata*, *Trichocerca multicrinis*, *Asplanchna priodonta*, *Kellicottia longispina*, *Polyarthra dolicoptera* and *P. remata* (Fig. 9). All of these species, with the exception of *P. dolicoptera*, were common between 1986 and 1992 (Lampman and Makarewicz 1999). The most abundant crustaceans during the sampling period included *Eubosmina coregoni*, *Bosmina longirostris*, *Daphnia retrocurva*, *Leptodora kindtii*, *Diacyclops thomasi* and copepod nauplii (Fig.10). Each of these species were common from 1986 to 1992 (Lampman and Makarewicz 1999) and 1981-1988 (Johannsson *et al.* 1991), with the exceptions of *E. coregoni*, which was never common and *L. kindtii*, which was only common from 1981-1988 (Johannsson *et al.* 1991). Observed differences between species abundances may be due to different locations of sampling (e.g. depth), different sampling methods (e.g. net size) or to *Cercopagis* establishment in 1998.

Cercopagis consumption of rotifer species does not appear to be energetically beneficial. *Cercopagis* must consume at least 20 times as many rotifer as cladoceran prey to achieve equivalent energy gain (Table 13). Using estimated bioenergetic requirements, at peak abundance the *Cercopagis* population could decimate much of the rotifer community within a few days (Table 13). Inverse abundance patterns of total rotifers and *Cercopagis* provide indirect evidence of *Cercopagis* predation. Historically, total rotifer abundance peaked from late July through August (Mazumder *et al.* 1992).

Overall, the total rotifer community could not assume a large proportion of *Cercopagis* dietary needs during its peak abundance due to their low overall energetic value and declining abundances.

Cercopagis consumption of cladoceran species would be more energetically beneficial. At its abundance peak, the *Cercopagis* population had the ability to consume between 30 and 1000 cladocerans*m^3*d^{-1}, depending on zooplankton size (Table 13). Overall cladoceran abundance at *Cercopagis*' peak abundance was low (Fig. 10). Inverse abundance patterns of these groups provides some evidence of *Cercopagis* predation.

Bosmina longirostris and *Leptodora kindtii* reached peak abundances by August 24th, even though *Cercopagis* abundance was >90 Ind./m^3. Initial depression in *Bosmina* abundance could be attributed to *Cercopagis* predation. However, *Bosmina* is also a preferred prey of *Leptodora*, thus its subsequent decline may have been due to increased abundance of this predator (Branstrator and Lehman 1991). Low abundances of both species may be attributed to intense *Cercopagis* predation. Overall, *Bosmina* abundance declined dramatically in 1999 at offshore sites in Lake Ontario as compared with historical abundances (C. Laxson, *pers. comm.*). *Leptodora* abundances have not changed since the early 1980's (C. Laxson, *pers. comm.*). Thus, it is plausible that *Cercopagis* caused the decline of *Bosmina* in the lake.

Daphnia retrocurva and *Diacyclops thomasi* abundances increased while *Cercopagis* abundances decreased (Fig. 10). Adult *Diacyclops* are unlikely to be a major prey of *Cercopagis* due to their large size, agility and presence in cooler water where *Cercopagis* is less abundant (Balcer *et al.* 1984). However, low densities of *Diacyclops* can be caused by high *Cercopagis* predation pressure on cyclopoid nauplii and copepodites.

Both cyclopoid nauplii and copepodite abundances declined dramatically in 1999 compared to historical abundance (Dr. O. Johannsson, *pers. comm.*) On the other hand, *Daphnia* is an excellent prey since its large, soft body and historically high abundance make it a suitable *Cercopagis* prey (Table 13). However, increasing *Daphnia* abundances in response to declining *Cercopagis* abundance provides only weak evidence for *Cercopagis* predation. Overall, *Daphnia* and *Diacyclops* abundances have declined after *Cercopagis* invasion in offshore Lake Ontario as compared to historical abundances (C. Laxson, *pers. comm.*).

Overall, *Cercopagis* predation pressure has affected both the temporal peak abundance and seasonal distributions of many zooplankton species in Lake Ontario.

Cercopagis laboratory predation

Assessment of species clearance rates and prey selectivity by *Cercopagis* in laboratory experiments may help clarify the potential impact of *Cercopagis* on zooplankton. However, the restrictive constraints of laboratory experiments may lead to inaccurate assumptions of predation effects (Vanderploeg *et al.* 1993). Previously, Mordukhai-Boltovskoi (1968) used small containers to describe feeding of *Cercopagis* on various zooplankton species. As well, Mordukhai-Boltovskaya (1958) used small containers to describe feeding of *Bythotrephes* on various zooplankton species. Vanderploeg *et al.* (1993) argued that small container studies are only useful to determine what can and cannot be eaten and that clearance rates and selectivity cannot be determined under such constrained conditions. The current study uses small containers to determine what prey may be eaten, as well as to determine clearance and consumption rate data. However, the

consumption rate data are supported by the correspondence between calculated values and results from bioenergetic modeling.

Cercopagis mortality was high in small containers and low in larger ones (Table 3, Table 4). *Cercopagis* mortality may have been caused by repeated contact with container walls, due to the small volume. As well, the clear glass walls in small containers, compared with frosted walls in the large containers, may be invisible to *Cercopagis* in the water column. However, *Cercopagis* acclimated in small containers had high survivorship (>95%) after 24hr. Therefore, swimming into walls may result from predatory behaviour, with attacking of prey leading to increased swimming speed and increased collisions with container walls.

Cercopagis prey clearance rates were higher in large containers then in smaller ones (Table 5). Increased clearance rates for large containers may be due to more efficient predation by *Cercopagis*. In large containers *Cercopagis* may visualize prey from a greater distance and attack before evasive actions are initiated. Consequently, larger containers may allow more natural predatory behaviour of *Cercopagis*.

Clearance rate was highest for *Asplanchna priodonta* in small containers (Table 5). Its relatively large size (~600μm), soft body and slow movement as compared to cladoceran species may render it more vulnerable to *Cercopagis*. Although body sizes of some cladoceran species presented were similar to *Asplanchna*, clearance rates in small container were at least 50% lower for all cladoceran species (Table 5). Decreased clearance rates may be due to increased motility of these cladoceran species. Higher motility should decrease capture efficiency of *Cercopagis*.

Cannibalistic interactions were discovered inadvertently during collection of *Cercopagis* in field samples. A single *Cercopagis* individual was found grasping and manipulating another *Cercopagis*, holding it from behind, while shredding and ingesting much of the body. Laboratory cannibalism events occurred only with 3rd instar *Cercopagis* individuals as predators (Table 6). *Cercopagis* may prey on conspecifics during peak abundances and potentially cause population decline. Extremely high abundances of *Cercopagis*, reaching up to 1,759 Ind./m^3 in 1999 (Makarewicz *et al.* 2001), also points to conspecifics as a possible food source. In the Dnieper-Bug (Ukraine) tidal estuary, average abundance reached 8,000 Ind./m^3 (Markovskii 1954), and peak abundance reached 26,000 Ind./m^3, creating a virtual *Cercopagis* monoculture (Polishchuk and Grigoriev 1989). In both instances, a cannibalistic lifestyle would be energetically valuable for *Cercopagis*.

Cercopagis in situ *field experiments*

Conditions were very similar in *in situ* experimental containers and in Lake Ontario. *In situ* experiments similar to the current study have been used to predict clearance rates for the predatory cladocerans *Bythotrephes* in Lake Huron (Vanderploeg *et al.* 1993) and *Mysis relicta* in Lake Michigan (Bowers and Vanderploeg 1982). However, natural conditions give rise to greater experimental variability. Results of my *in situ* field experiments were unsuccessful in clarifying *Cercopagis* predation effects on the lake zooplankton community.

During the early summer, the *Cercopagis* population in Lake Ontario was composed of a high proportion of 1st and 2nd instar individuals (>90%). The importance of these early

instar stages has not been a point of emphasis in the current study, however, consumption by 1st and 2nd instar stages could be important to the zooplankton community. The first two instar stages of *Bythotrephes* have been shown to account for approximately 44% of an individuals' total lifetime prey consumption (Yurista and Schulz 1995).

Although the early instar stages are important, 3rd instar *Cercopagis* were dominant during population maxima in Lake Ontario during 1998, 1999 and 2000 (MacIsaac *et al.* 1999). Third instar *Cercopagis* have been shown to dominate in all *Cercopagis* populations at some times (Grigorovich *et al.* 2000). Overall dominance during peak abundances and high per capita predation rates make 3rd instar *Cercopagis* the most important individuals for assessing predatory impact.

Individual field experiments were performed for each of the three *Cercopagis* instars (Tables 8, 9). Separate experiments were performed for each instar, since the proportional and total consumption rates and prey preference will change with each subsequent *Cercopagis* instar change. *Bythotrephes* exhibits a decreasing percentage of body mass being eaten, yet increasing total consumption, with each successive instar (Yurista and Schulz 1995, Lehman and Branstrator 1995). However, no differences between instar stages were found owing to unsuccessful field experiments.

Field experiments were attempted on 4 separate occasions without success. No effects of *Cercopagis* predation were found in any of the experiments (Tables 8, 9, 10, 11). Design changes were made after each experiment in an attempt to identify and resolve possible problems in experimental design. The lack of predation evidence in all natural assemblage experiments is an artifact. Potential problems include: improper light conditions for predatory behaviour, turbulent water currents within the containers due to

trapped air, stress on *Cercopagis* due to handling, negative interference between *Cercopagis* conspecifics, mortality of *Cercopagis* individuals, or any combination thereof.

Opaque carboy containers were used in the first two field experiments during 2000. *Cercopagis* is a visual predator, therefore it requires light to search for prey (K. McPhedran, *unpublished data*). Otherwise, only incidentally contacted prey could be captured and eaten. In a similar study involving *Bythotrephes*, clear plexiglass containers were used with screened light, in a modified *in situ* experiment (Vanderploeg *et al.* 1993). Containers were changed to clear plastic for experiments #3 and #4. Although these containers allow entrance of ambient light, this amendment did not result in successful experiments.

Removal of air from each carboy in the first two field experiments was unsuccessful. This was due to carboy handles attached within the container volume, which made complete removal of air impossible. Trapped air produces water currents which make swimming and predation attempts difficult for *Cercopagis*. Containers used in experiments #3 and #4 were filled completely, with no trapped air present.

Cercopagis collection may have stressed individuals, causing mortality or a subsequent inability to acclimate to conditions in the experimental containers. *Cercopagis* may have needed more time to acclimate to the container environment prior to feeding, as in the acclimation period needed within laboratory experiments. *Cercopagis* may have used the entire experimental duration for acclimatizing to the container environment, rather than feeding on prey. However, the extension of the experimental duration to 48 hours for

experiment #4 was also unsuccessful in producing predation effects. Acclimation prior to use in field experiments may be needed in further studies.

Negative interference or cannibalism may have occurred in experimental containers. Although possible, the container sizes and *Cercopagis* densities make interference unlikely. However, if individuals became entangled by their caudal appendages, inadvertent stress or death could result (K. McPhedran, *unpublished data*).

The quantity of prey organisms eaten may not have been great enough to detect significant differences in feeding trials. The number of *Cercopagis* in experimental containers may have been too low to have statistically significant effects on zooplankton composition. As well, if *Cercopagis* is omnivorous, individual species predation may not have been empirically quantified. Vanderploeg *et al.* (1993) added 60 *Bythotrephes* to 30L experimental containers. The large size of *Bythotrephes* leads to much higher consumption rates. Therefore, too few *Cercopagis* may have been used in experimental treatments. Unfortunately, increasing *Cercopagis* density leads to increased risks of cannibalism and negative interference.

Lastly, *Cercopagis* mortality may have reduced discernible predation effects. Assuring that *Cercopagis* were alive at the end of the experimental duration was impossible. The water volume and replication made searching for live *Cercopagis* prior to preservation impossible.

In summary, despite apparent effects on specific taxa in Lake Ontario, my field studies uncovered no repeatable predation effects by *Cercopagis* on any zooplankton species.

Summary

Results of this study indicate that *Cercopagis* has affected the native zooplankton of Lake Ontario. *Cercopagis* has decreased abundances of the crustaceans *Bosmina longirostris*, *Daphnia retrocurva*, *Diacyclops thomasi* and total rotifers. *Cercopagis* has become an energetic link in Lake Ontario by consuming herbivorous zooplankton, and in turn being eaten by alewife.

In the laboratory environments, *Cercopagis* had the ability to prey upon numerous zooplankton species, including the rotifer *Asplanchna priodonta* and the cladocerans *B. longirostris*, *D. retrocurva*, *C. lacustris*, *S. kingi*, *M. micrura* and *L. kindtii*. *Cercopagis* preys on zooplankton by grasping and shredding the body and consuming the soft-body pieces. Consumption rates determined in laboratory experiments closely approximated bioenergetic model estimations.

Despite numerous attempts, *in situ* field experiments were unsuccessful. Significant *Cercopagis* predation of zooplankton was not demonstrated in any experimental predation treatment.

Cercopagis has apparently become an energetic link in Lake Ontario. It has increased the efficiency of energy transfer in Lake Ontario by becoming a food source of the alewife, which is the dominant planktivore. Further spread of *Cercopagis* in the Great Lakes basin and beyond is imminent.

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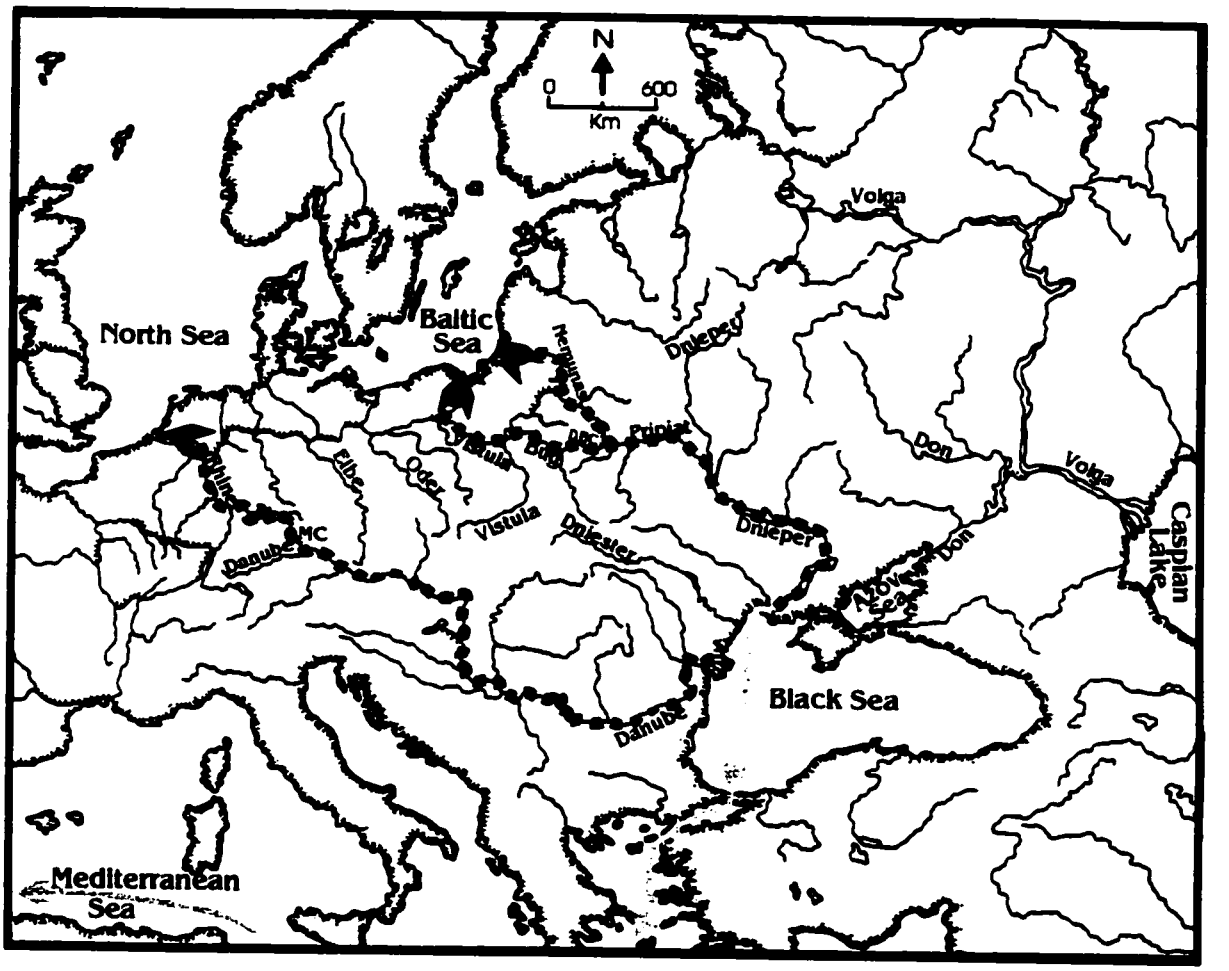


Figure 1. Proposed 'invasional corridors' used to transport Ponto-Caspian species throughout Europe and beyond. Transport may be through shipping freighters, recreational boating or through natural diffusive expansion. From MacIsaac *et al.* (*in press*, 2001)

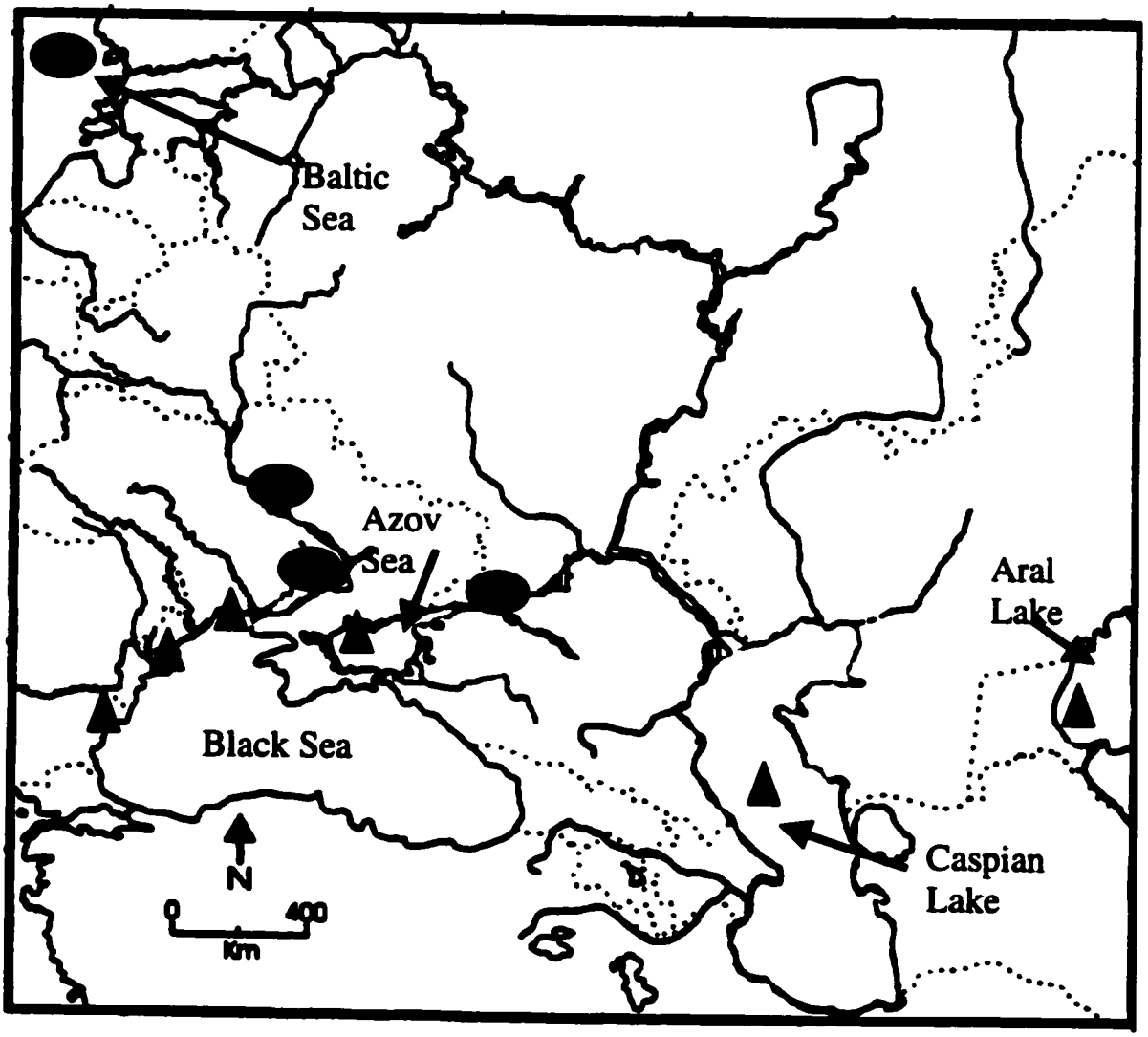


Figure 2. The Eurasian distribution of *Cercopagis pengoi*. Native regions are denoted with solid triangles and invaded regions are denoted by ovals. Invaded regions include reservoirs and canals of the Dnieper, Don, and Manych rivers and the Baltic Sea.

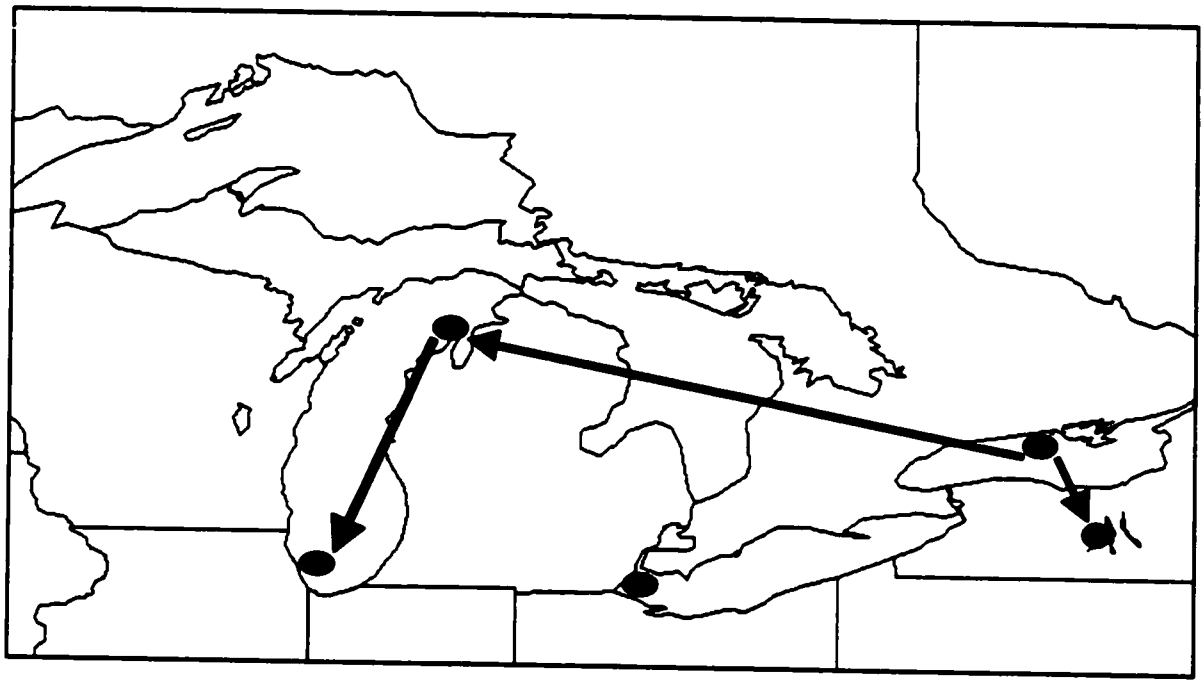


Figure 3. The spread of *Cercopagis pengoi* in the Great Lakes region. Records of first invasion were during 1998 in Lake Ontario. Further spread to the Finger Lakes region of northern New York State and to Lake Michigan occurred in 1999 and to Lake Erie in 2001 (Dr. I Grigorovich, *pers. comm.*).

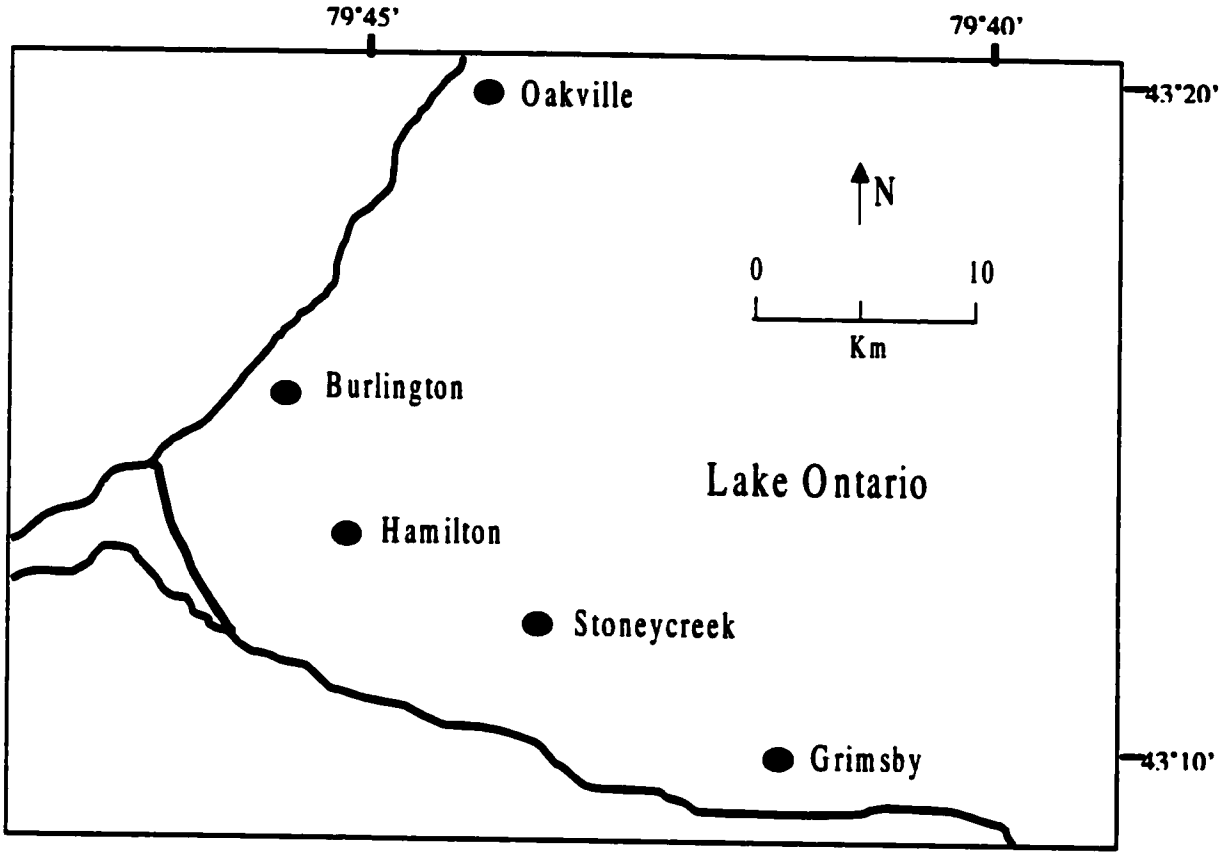


Figure 4. Location of sampling sites in western Lake Ontario during the years 1999-2001. All sites were sampled with both 53μm and 253μm Nitex mesh plankton nets. Physicochemical values were also assessed at each sample site.

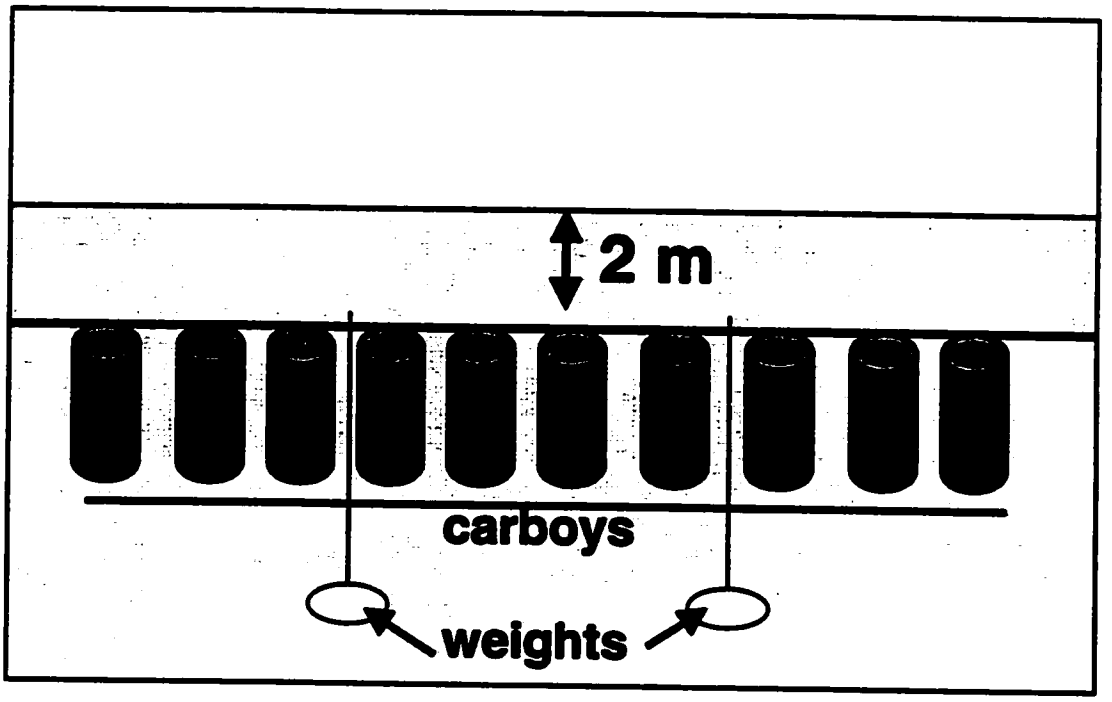


Figure 5. Field experimental setup of carboys. Rope and weights were used to keep carboys at approximately 2m below the water surface.

Figure 6. Experimental design of *in situ* field experiments. Design used for all year 2000 *Cercopagis* field experiments. See text for year 2001 field experiment changes.

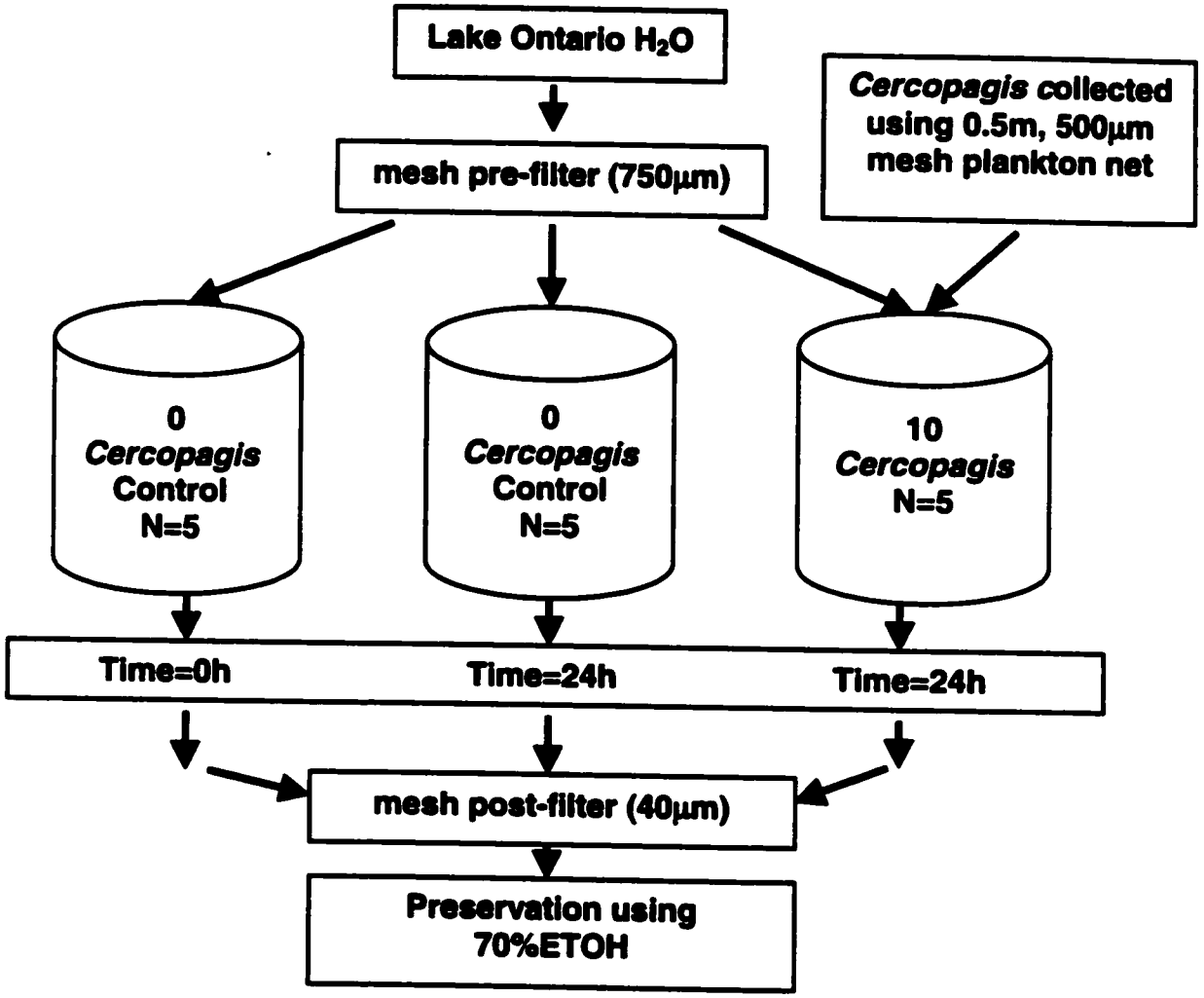

Lake Ontario H_2O
mesh pre-filter (750μm)
Cercopagis collected using 0.5m, 500μm mesh plankton net
0 *Cercopagis* Control N=5
0 *Cercopagis* Control N=5
10 *Cercopagis* N=5
Time=0h
Time=24h
Time=24h
mesh post-filter (40μm)
Preservation using 70%ETOH

Figure 7. Mean (±SE) values of dissolved oxygen (mg/L) and temperature (°C) versus depth of the combined sampling sites (N=5) in western Lake Ontario during summer 2000.

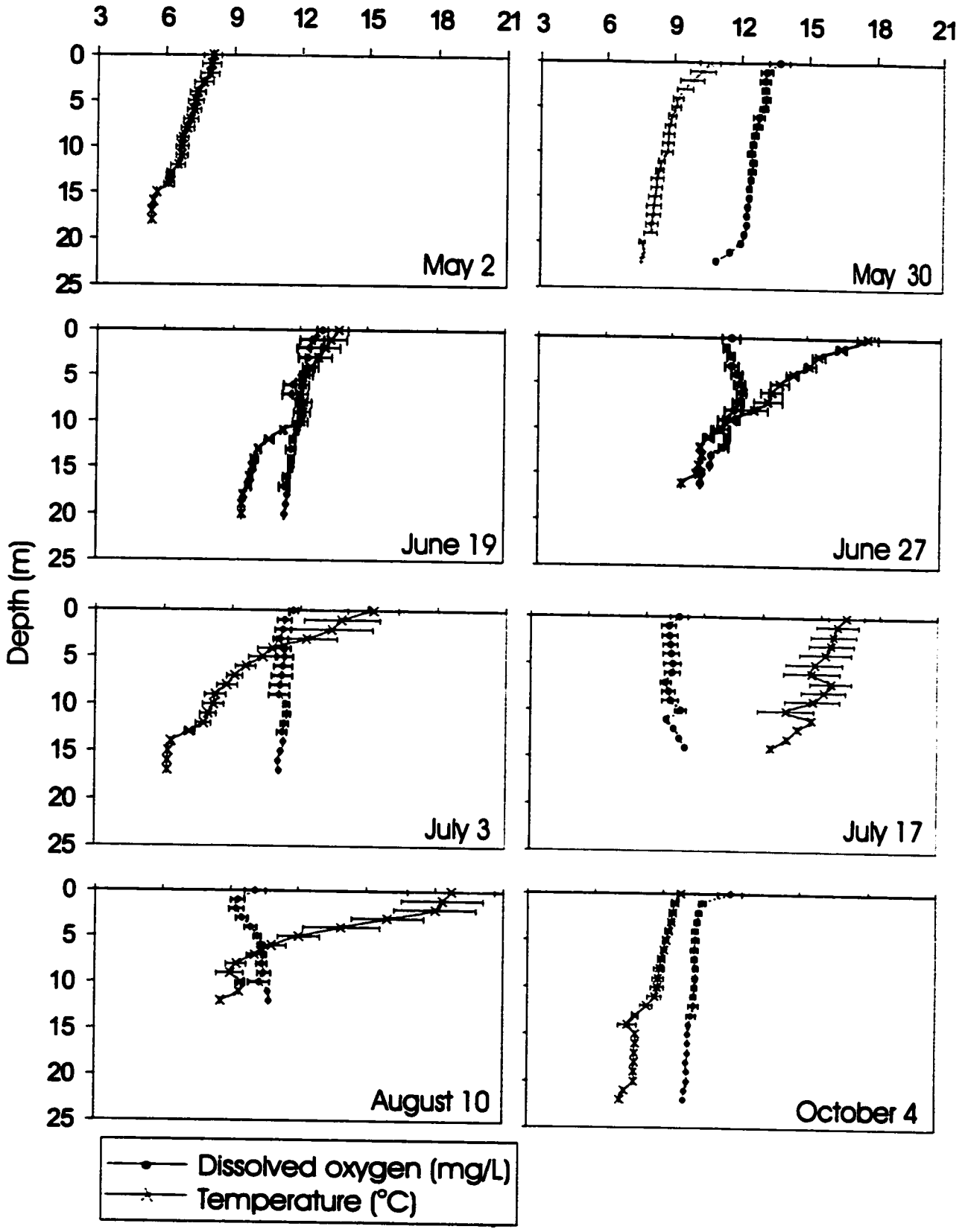

3 6 9 12 15 18 21
0 5 10 15 20 25
Depth (m)
May 2
May 30
June 19
June 27
July 3
July 17
August 10
October 4
Dissolved oxygen (mg/L)
Temperature (°C)

Figure 8. Mean (±SE) values of conductivity (µs/cm) versus depth of the combined sampling sites (N=5) in western Lake Ontario during summer 2000.

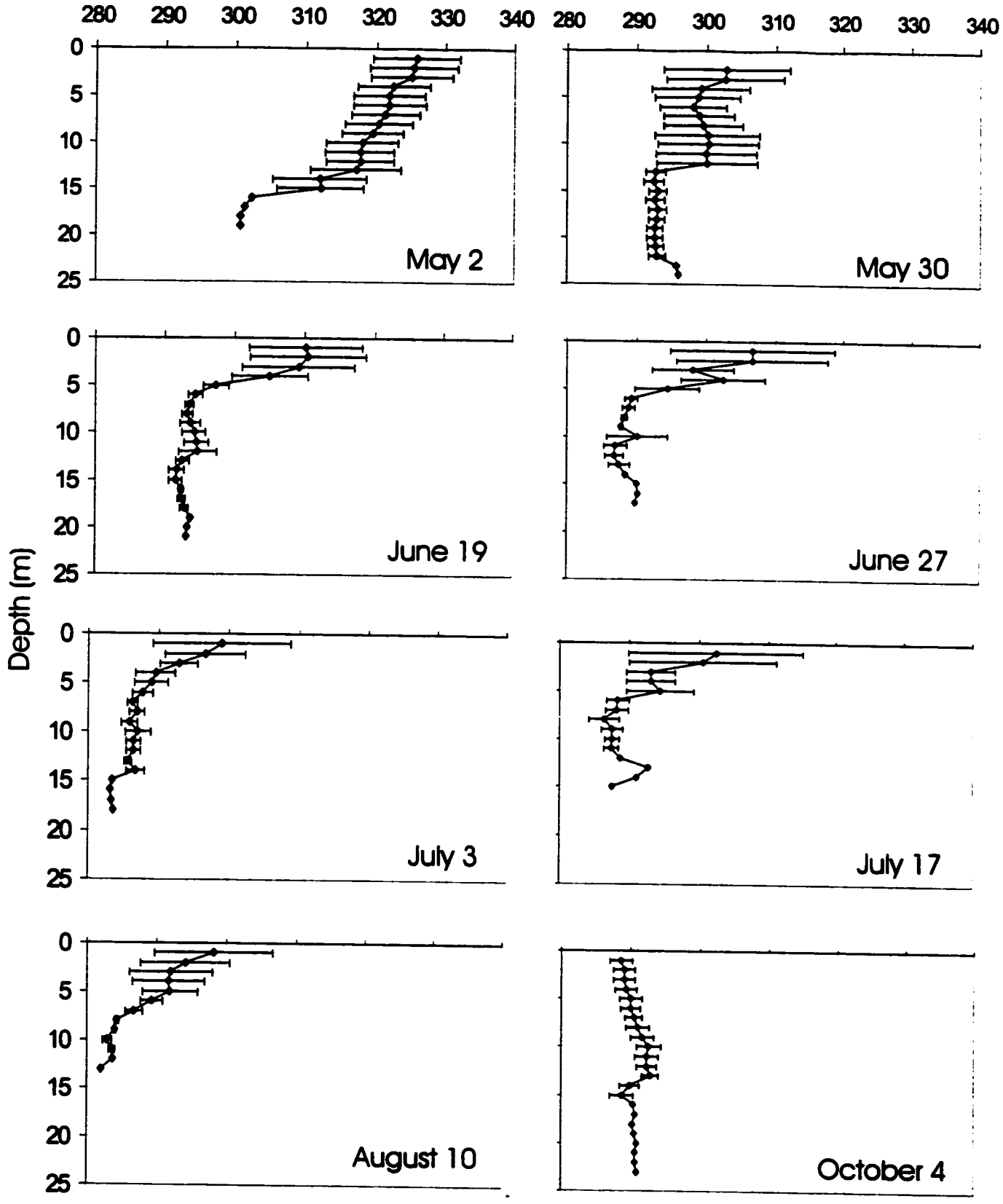

280
290
300
310
320
330
340
0
5
10
15
20
25
Depth (m)
May 2
May 30
June 19
June 27
July 3
July 17
August 10
October 4

Figure 9. Mean abundance (± S.E.) of the most abundant rotifer species and total rotifers. Samples collected on dates from April through October 2000. Values are averages of separate sampling sites (N=5).

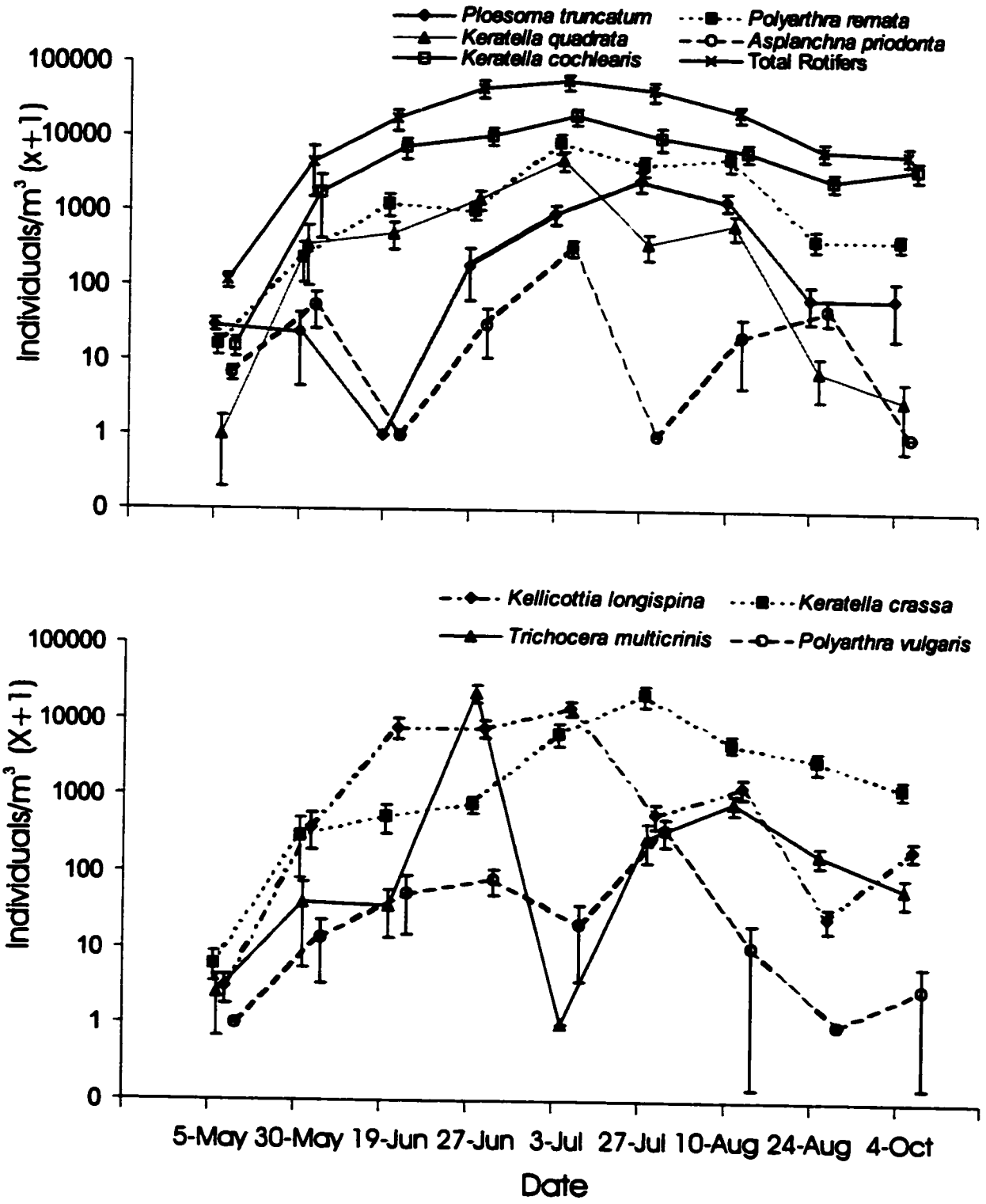
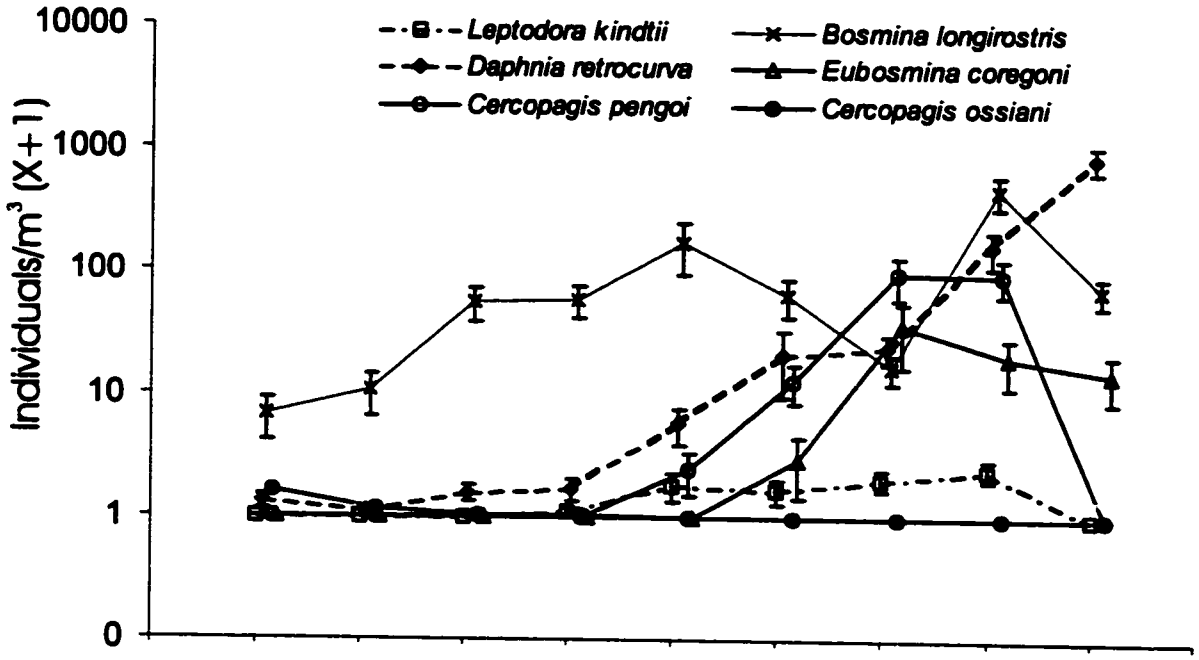

Ploesoma truncatum
Polyarthra remata
Keratella quadrata
Asplanchna priodonta
Keratella cochlearis
Total Rotifers
Individuals/m³ (x+1)
100000
10000
1000
100
10
1
0
Kellicottia longispina
Keratella crassa
Trichocera multicrinis
Polyarthra vulgaris
Individuals/m³ (X+1)
5-May 30-May 19-Jun 27-Jun 3-Jul 27-Jul 10-Aug 24-Aug 4-Oct
Date

Figure 10. Mean abundance (± S.E.) of cladocerans, total cladocerans, copepods, copepod nauplii and *Cercopagis*. Samples collected on dates from April through October 2000. Values are average of separate sampling sites (N=5).


10000
1000
100
10
1
0
Individuals/m³ (X+1)
Leptodora kindtii
Bosmina longirostris
Daphnia retrocurva
Eubosmina coregoni
Cercopagis pengoi
Cercopagis ossiani

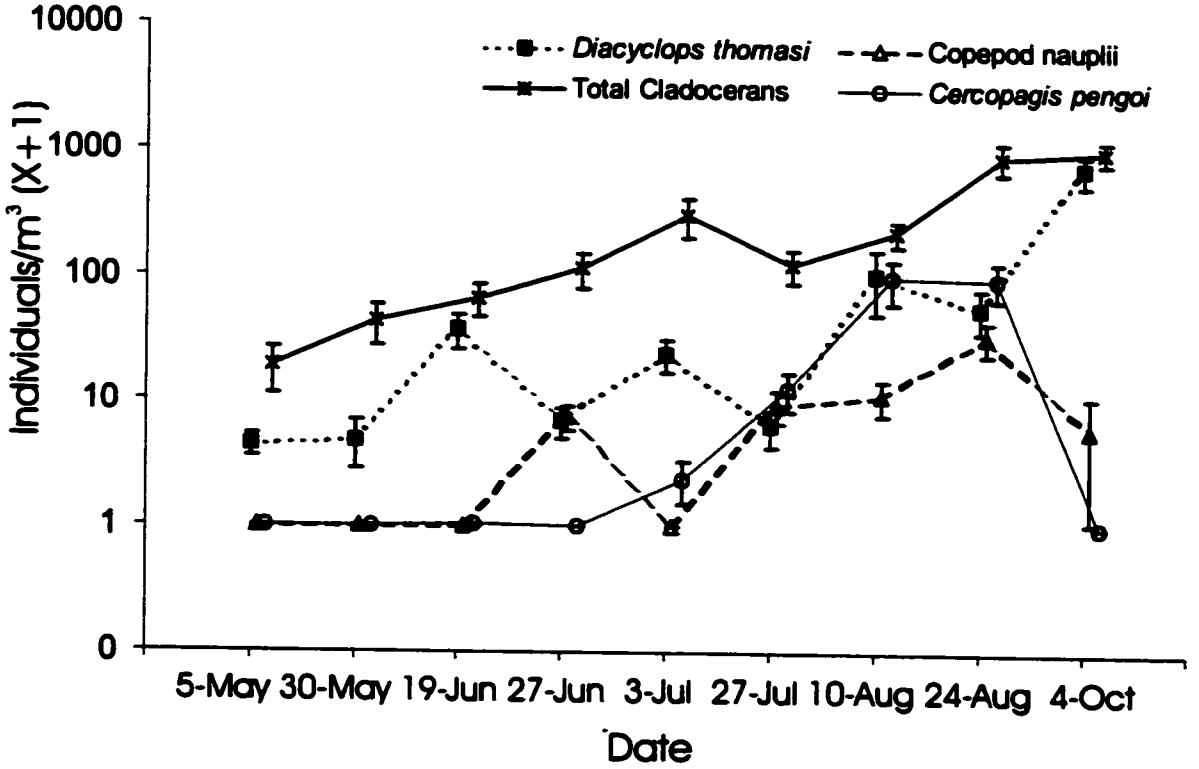

10000
1000
100
10
1
0
Individuals/m³ (X+1)
Diacyclops thomasi
Copepod nauplii
Total Cladocerans
Cercopagis pengoi
5-May
30-May
19-Jun
27-Jun
3-Jul
27-Jul
10-Aug
24-Aug
4-Oct
Date

Figure 11. Relative prey preference of *Cercopagis* versus mean (±S.E.) prey body size. Preferences based on small container experiments using Manly's α electivity index.

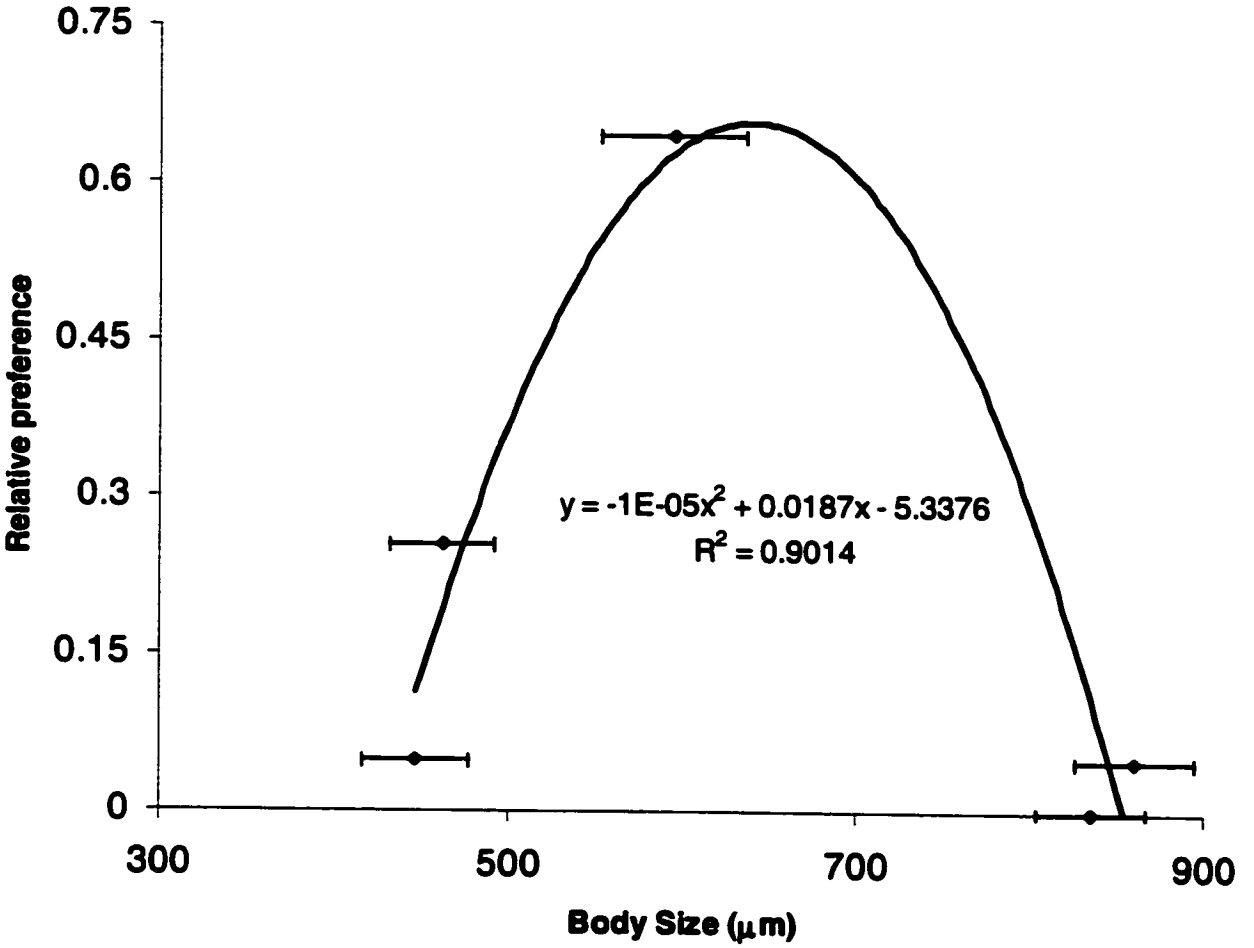

0.75
0.6
0.45
0.3
0.15
0
Relative preference
y = -1E-05x2 + 0.0187x - 5.3376
R2 = 0.9014
300
500
700
900
Body Size (µm)

Table 1. Mean (± S.E.) of physiochemical properties for five sites in western Lake Ontario. Values are averages for the whole water column or for the epilimnion, when present.

Parameter	*May*	*June*	*July*	*August*	*September*	*October*
pH	9.1±0.5	9.7±0.3	9.7±0.4	9.4±0.4	ND	9.3±0.2
Conductivity (μs/cm)	307.9±15.9	295.4±11.7	292.2±13.0	289.5±10.1	ND	290.3±2.9
Secchi depth (m)	4.5±1.3	3.6±0.6	5.45±1.0	5.7±1.0	ND	5.5±1.3
Total Dissolved Solids (mg/L)	196.1±13.1	189.2±7.6	186.0±6.9	185.1±6.0	ND	185.9±1.9
Site depth (m)	16.4±2.3	16.0±3.1	16.0±2.4	15.4±3.3	ND	14.7±3.7

Table 2. Maximum abundance for each rotifer, cladoceran and copepod species and their percentage composition of the total community (rotifer species and cladoceran+copepod species considered separately).

Species	Ind./m^3	SE	Date	% of Total
		Rotifers		
Asplanchna priodonta	335	82	July 3	<1
Kellicottia longispina	14625	3369	July 3	25.3
Keratella cochlearis	19527	4989	July 3	33.9
Keratella crassa	21904	6590	July 27	51.2
Keratella quadrata	4931	1374	July 3	8.5
Ploesoma truncatum	2728	822	July 27	6.4
Polyarthra dolicoptera	669	156	July 3	1.1
Polyarthra remata	8598	2421	July 3	14.9
Polyarthra vulgaris	372	142	July 27	1
Trichocerca multicrinis	22689	6119	June 27	50.0
		Cladocerans		
Bosmina longirostris	475	143	August 24	49.6
Cercopagis pengoi	96	36	August 10	29.6
Daphnia retrocurva	875	216	October 4	50.6
Eubosmina coregoni	35	19	August 10	10.8
Leptodora kindtii	2	0	August 24	<1
		Copepods		
Diacyclops thomasi	730	201	October 4	42.2
Copepod nauplii	32	9	August 24	3.4

Table 3. *Cercopagis* interactions with five potential prey species, in small vials (150ml) in laboratory experiments. All trials were initiated with 10 prey and were 18 hours in duration. [1] denotes prey damaged due to predation [2] denotes possible whole prey feeding.

Treatment	Replicate	End number of prey individuals		*Cercopagis* Condition	Missing prey
		Alive	Dead		
Ceriodaphnia lacustris	1	9	1	DEAD	0
	2	10	0	DEAD	0
	3	10	0	LIVE	0
	Control	10	0	n/a	0
Asplanchna priodonta	1	7	1	DEAD	2[2]
	2	8	0	DEAD	2[2]
	3	4	6	DEAD	0
	Control	10	0	n/a	0
Moina micrura	1	9	1	LIVE	0
	2	11	3	LIVE	0
	3	12	2	DEAD	0
	Control	12	0	n/a	0
Scapheloberis kingi	1	9	0	LIVE	1[2]
	2	5	2	LIVE	3[2]
	3	11	1	DEAD	0
	Control	10	0	n/a	0
Daphnia retrocurva	1	8	1[1]	DEAD	1[2]
	2	9	2[1]	DEAD	0
	3	9	1[1]	DEAD	0
	Control	9	1	n/a	0

Table 4. *Cercopagis* interactions with three potential prey species in large vessel (1.5L) laboratory experiments. All trials were initiated with 40 prey and were 12 hours in duration. Brackets denote organisms found in surface film.

TREATMENT	Replicate	End number of prey individuals			*Cercopagis* condition
		Alive	Dead	Eaten	
Ceriodaphnia lacustris					
Control	1	37	3	--	--
	2	37	1	--	--
	3	40	0	--	--
	4	37	1	--	--
	5	40	0	--	--
Cercopagis	1	46	1	0	DEAD
	2	41	0	2	ALIVE
	3	44	0	0	ALIVE
	4	42	0	2	DEAD
	5	45	0	0	ALIVE
Daphnia retrocurva					
Control	1	36	4	--	--
	2	35	5	--	--
	3	38(3)	2	--	--
	4	39(1)	3	--	--
Cercopagis	1	31(2)	1	3	ALIVE
	2	29(3)	1	2	ALIVE
	3	46(3)	3	0	ALIVE
	4	34(1)	1	1	ALIVE
	5	41(3)	0	0	DEAD
Bosmina longirostris					
Control	1	29	3	--	--
	2	38(1)	1	--	--
	3	40(2)	1	--	--
	4	34(2)	1	--	--
Cercopagis	1	29	1	0	ALIVE
	2	41	0	0	ALIVE
	3	30(2)	0	0	ALIVE
	4	40(2)	0	1	ALIVE
	5	34(1)	2	1	ALIVE

Table 5. Consumption rates (Ind./*Cercopagis*/day) and clearance rates (L/*Cercopagis*/day) of *Cercopagis* on different prey species. Clearance rates were estimated based upon experiments conducted in small containers.

Species	Consumption rate (Ind./*Cercopagis*/day)		Clearance rate*10^{-2} (L/*Cercopagis*/day)		Relative Preference
	Small	Large	Small	Large	
Bosmina longirostris	--	2.8	--	11.3	--
Ceriodaphnia lascustris	1.3	0	0.7	0	0.05
Scapheloberis kingi	6.6	--	3.6	--	0.26
Asplanchna priodonta	14.7	--	9.1	--	0.65
Moina micrura	0	--	0	--	0
Daphnia retrocurva	1.3	2.8	0.7	10.7	0.05

Table 6. Interactions between *Cercopagis* in small containers (150ml) for 24 hours. Bold text denotes deaths ascribed to cannibalism (see text for details). Instar changes due to moulting are noted in brackets.

Start		**End**	
Individual #1 instar	Individual #2 instar	*Cercopagis* #1	*Cercopagis* #2
1^{st}	2^{nd}	ALIVE (2^{nd} instar)	ALIVE (3^{rd} instar)
1^{st}	2^{nd}	DEAD	ALIVE
1^{st}	2^{nd}	***DEAD*** [spine and head]	ALIVE (3^{rd} instar)
1^{st}	2^{nd}	ALIVE	ALIVE
1^{st}	2^{nd}	DEAD	DEAD
2^{nd}	3^{rd}	DEAD	ALIVE
2^{nd}	3^{rd}	DEAD (3^{rd} instar)	DEAD
2^{nd}	3^{rd}	DEAD (3^{rd} instar)	DEAD
2^{nd}	3^{rd}	***DEAD*** [3^{rd} instar spine]	ALIVE
2^{nd}	3^{rd}	ALIVE	ALIVE
1^{st}	3^{rd}	ALIVE (2^{nd} instar)	ALIVE
1^{st}	3^{rd}	ALIVE (2^{nd} instar)	ALIVE
1^{st}	3^{rd}	ALIVE	DEAD
1^{st}	3^{rd}	ALIVE (2^{nd} instar)	ALIVE
1^{st}	3^{rd}	ALIVE (2^{nd} instar)	ALIVE

Table 7. Mean (±S.E.) densities of manipulated field assemblages of a single 3rd instar *Cercopagis* with four zooplankton prey species in clear containers (2L) deployed in Lake Ontario for 18 hours. All trials were initiated with 15 prey from each species for a total of 60 prey/container. SF= caught in surface film.

Species	Control (n=5)						*Cercopagis* treatment (n=5)					
	Alive	S.E.	Dead	S.E.	SF	S.E.	Alive	S.E.	Dead	S.E.	SF	S.E.
Daphnia retrocurva	13.2	1.4	1.4	0.5	1.0	0.3	12.5	1.5	0.5	0.5	0.8	0.3
Ceriodaphnia lacustrus	15.2	1.2	0.2	0.1	NA	NA	14.8	1.3	0.0	0.0	NA	NA
Bosmina longirostris	12.6	1.5	0.8	0.4	3.2	0.6	12.8	1.7	0.5	0.5	2.5	0.6
Chydorus sphaericus	13.2	1.7	0.6	0.2	NA	NA	8.5	1.9	0.3	0.3	NA	NA
Total prey (alive+dead+SF)	61.4±2.7						53.0±3.0					

Table 8. Field Experiment #1: Mean (Ind./L ± S.E.) abundance of rotifers, cladocerans, copepods, copepod nauplii and *Dreissena* veligers present in the field experiment with 3rd instar *Cercopagis*. Carboys (22.75L) were deployed in Lake Ontario for 24 hours on August 9, 2000.

	0 hour treatment		24 hour treatments			
	Control		*Control*		*3rd instar Cercopagis*	
Species	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**
Keratella quadrata	3.1	1.3	4.4	1.7	5.1	0.9
Keratella cochlearis	79.6	11.8	62.2	6.4	68.6	7.7
Keratella crassa	63.4	4.5	60.1	6.6	53.6	4.7
Trichocerca multicrinis	7.7	0.8	9.4	1.0	13.3	0.2
Asplachna priodonta	3.2	0.5	2.3	0.7	2.3	0.2
Kellicottia longispina	6.8	2.1	4.4	1.2	6.9	1.0
Ploesoma truncatum	15.6	3.0	24.2	5.9	16.2	1.6
Polyarthra remata	69.2	13.1	34.6	6.8	47.5	7.7
Polyarthra dolicoptera	27.0	10.1	20.8	4.5	21.9	1.6
OTHER	5.0	2.1	4.6	1.6	3.2	0.9
Total Rotifers	351.9	38.1	226.8	24.8	238.7	6.3
Bosmina longirostris	13.6	5.8	4.0	0.9	4.1	0.6
Chydorus sphaericus	1.0	0.6	0.7	0.3	0.4	0.3
Daphnia retrocurva	0.1	0.1	0.0	0.0	0.0	0.0
Total Cladocerans	14.37	6.0	12.3	3.3	13.7	2.0
Cyclopoid copepods	7.8	1.2	7.6	2.1	7.7	0.6
Copepod nauplii	51.2	5.1	30.1	2.0	42.1	0.9
***Dreissena* veligers**	8.4	2.5	6.3	1.3	6.9	1.6
Total Organisms	431.4	51.5	275.6	30.8	301.3	4.0

Table 9. Field Experiment #2: Mean (Ind./L ± S.E.) abundance of rotifers, cladocerans, copepods, copepod nauplii and *Dreissena* veligers present in the field experiment with 1st and 2nd instar *Cercopagis*. Carboys (22.75L) were deployed in Lake Ontario for 24 hours on August 14, 2000.

	0 hour treatment		24 hour treatments					
	Control		*Control*		*1st instar Cercopagis*		*2nd instar Cercopagis*	
Species	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**
Keratella cochlearis	3.7	0.8	2.5	1.0	2.0	0.4	1.9	0.7
Keratella crassa	9.8	0.7	12.0	0.8	11.0	1.7	13.6	1.0
Trichocerca multicrinis	0.8	0.5	1.1	0.2	1.9	0.2	0.6	0.2
Asplachna priodonta	0.0	0.0	0.3	0.1	0.3	0.2	0.6	0.2
Ploesoma truncatum	3.7	1.3	4.2	0.3	4.2	1.0	4.8	0.4
Polyarthra remata	28.9	2.4	15.9	1.0	11.3	1.7	18.0	5.5
Polyarthra vulgaris	0.6	0.6	0.3	0.1	0.0	0.0	0.2	0.1
Lecane luna	1.4	0.8	1.1	0.4	0.7	0.2	0.6	0.5
Ascomorpha sultans	2.1	0.5	5.7	0.5	4.4	0.8	4.6	1.7
Total Rotifers	52.4	6.3	44.3	1.9	37.6	3.4	45.7	4.9
Bosmina longirostris	14.9	0.8	17.9	2.5	18.2	2.6	16.3	3.5
Chydorus sphaericus	1.0	0.3	1.1	0.2	1.7	0.3	1.3	0.1
Polyphemus pediculus	1.3	0.6	0.7	0.4	3.3	0.6	1.3	0.2
Other	0.3	0.1	0.2	0.1	0.1	0.1	0.4	0.1
Total Cladocerans	17.5	1.9	20.1	2.5	23.5	2.3	19.5	3.7
Cyclopoid copepods	0.0	0.0	0.2	0.0	0.2	0.1	0.2	0.1
Copepod nauplii	1.8	0.1	1.6	0.7	2.3	0.5	2.8	0.5
***Dreissena* veligers**	1.1	0.4	1.2	0.3	1.8	0.8	1.7	0.6
Total Organisms	72.0	5.2	67.1	1.8	65.2	5.5	69.7	7.4

Table 10. Field Experiment #3: Mean (Ind./L ± S.E.) abundance of rotifers, cladocerans, copepods and copepod nauplii present in the field experiment with 3rd instar *Cercopagis*. Containers (4L) were deployed in Lake Ontario for 24 hours on July 5, 2001.

	0 hour treatment		24 hour treatments			
	Control		*Control*		*3rd instar Cercopagis*	
Species	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**
Polyarthra remata	129.0	21.2	112.5	11.1	146.6	29.2
Ascomorpha sultans	28.3	6.7	27.1	7.1	29.3	6.3
Polyarthra major	137.1	37.7	219.0	36.2	245.9	35.8
Synchaeta lakowicz	32.4	4.6	19.3	5.6	33.2	14.3
Ploesoma truncatum	154.9	23.6	131.7	24.9	145.9	21.2
Keratella cochlearis	14.8	3.3	13.9	6.0	15.0	6.6
Kellicottia longispina	3.5	2.6	3.5	2.6	7.6	3.5
Trichocerca multicrinis	0.0	0.0	2.8	0.8	6.7	3.6
Asplachna priodonta	9.9	0.1	12.8	0.8	12.6	0.8
Total Rotifers	512.2	79.1	542.6	90.9	642.8	113.7
Bosmina longirostris	13.3	0.9	15.0	0.4	12.8	1.3
Polyphemus pediculus	4.3	0.6	3.8	0.6	4.5	1.4
Chydorus sphaericus	1.1	0.2	1.0	0.0	0.8	0.1
Ceriodaphnia lacustris	0.8	0.3	1.5	0.3	0.8	0.3
Daphnia retrocurva	0.4	0.1	0.5	0.3	0.1	0.1
Diaphanosoma birgei	1.8	0.3	2.5	0.1	2.0	0.3
Total Cladocerans	22.7	0.9	24.3	1.0	20.9	2.7
Cyclopoid copepods	5.3	0.3	4.9	0.3	4.8	0.4
Copepod nauplii	4.2	1.3	7.0	2.1	3.8	1.4
Total Organisms	543.5	79.5	578.8	90.9	669.5	116.1

Table 11. Field Experiment #4: Mean (Ind./L ± S.E.) abundance of rotifers, cladocerans, copepods and copepod nauplii present in the field experiment with 1st and 2nd instar *Cercopagis*. Containers (4L) were deployed in Lake Ontario for 24 hours on August 2, 2001.

	0 hour treatment		48 hour treatments					
	Control		*Control*		*4-3rd instar Cercopagis*		*8-3rd instar Cercopagis*	
Species	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**	**Ind./L**	**SE**
Keratella cochlearis	3.1	1.8	2.6	0.9	3.2	1.2	7.0	1.7
Keratella crassa	17.0	6.7	18.7	4.2	17.4	5.4	20.1	1.4
Trichocerca multicrinis	1.6	1.1	1.2	0.8	0.5	0.6	0.7	0.4
Ploesoma truncatum	135.4	26.3	257.6	12.0	223.1	42.2	223.4	12.4
Polyarthra remata	155.0	22.0	405.0	63.3	421.4	86.3	422.1	54.1
Polyarthra vulgaris	14.3	4.9	20.9	6.0	15.6	7.0	10.7	3.2
Polyarthra major	63.1	9.9	90.7	30.6	58.0	11.5	31.5	6.6
Total Rotifers	389.3	38.9	796.8	107	739.1	141	714.9	73.3
Bosmina longirostris	143.3	5.9	187.7	2.7	219.7	24.4	195.0	13.5
Total Cladocerans	143.3	5.9	187.7	2.7	219.7	24.4	195.0	13.5
Cyclopoid copepods	9.7	2.3	28.3	3.3	26.0	2.8	22.7	1.1
Copepod nauplii	12.3	2.2	12.7	1.8	12.3	1.6	12.7	1.1
Total Organisms	554.7	35.6	1025.4	105	997.1	118	945.2	84.3

Table 12. Analysis of variance of abundances of total rotifers, total cladocerans, total copepods, *Dreissena* veligers, copepod nauplii and total organisms (values ln X+1 transformed). *Cercopagis* treatment was the independent, categorical variable for all analyses. MANOVA tests explored variation in all zooplankton taxa simultaneously as a function of *Cercopagis* treatment.

Field Experiment	Independent Variable	df	F	p
#1	Total rotifers	2,6	6.98	<0.05
	Total cladocerans	2,6	0.05	0.944
	Total copepods	2,6	0.22	0.808
	Dreissena veligers	2,6	14.4	<0.05
	Copepod nauplii	2,6	3.41	0.103
	Total organisms	2,6	2.21	0.191
MANOVA	Wilks' lambda= 0.002	2,12	1.14	0.441
#2	Total rotifers	3,8	1.82	0.221
	Total cladocerans	3,8	2.29	0.155
	Total copepods	3,8	0.35	0.793
	Dreissena veligers	3,8	3.01	0.095
	Copepod nauplii	3,8	0.51	0.688
	Total organisms	3,8	0.57	0.653
MANOVA	Wilks' lambda= 0.035	8,18	3.31	0.255
#3	Total rotifers	1,7	0.63	0.454
	Total cladocerans	1,7	0.23	0.646
	Total copepods	1,7	0.05	0.824
	Copepod nauplii	1,7	0.03	0.878
	Total organisms	1,7	0.91	0.372
MANOVA	Wilks' lambda= 0.219	3,5	2.13	0.283
#4	Total rotifers	3,8	8.44	<0.05
	Total cladocerans	3,8	8.08	<0.05
	Total copepods	3,8	14.6	<0.05
	Copepod nauplii	3,8	0.03	0.99
	Total organisms	3,8	11.8	<0.05
MANOVA	Wilks' lambda= 0.017	11,15	2.55	0.058

Table 13. Estimated number of prey species that would be required to fulfill a single *Cercopagis pengoi*'s consumption needs based upon bioenergetic considerations. Peak consumption by *Cercopagis* is based upon highest recorded *Cercopagis* abundance during summer 2000 field samples. The analysis is based upon Yurista and Schulz's (1995) study of *Bythotrephes*. Zooplankton weights and lengths were taken from Bottrell *et al.* (1976) and Culver *et al.* (1985).

Prey species	Prey/*Cercopagis*/day	Prey/*Cercopagis*/day at peak *Cercopagis* abundance
Asplanchna priodonta	18	1687
Keratella cochlearis	118	11332
Polyarthra vulgaris	198	18977
Bosmina longirostris	6	561
Ceriodaphnia lacustris	11	1032
Chydorus sphaericus	8	803
Daphnia retrocurva	2	151
Eubosmina coregoni	3	303
Leptodora kindtii	~1	31
Copepod nauplii	36	3458

Vita Auctoris

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